# Life-history, ecology and fisheries of cephalopods in the western Mediterranean

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*Für meine Eltern, in Dankbarkeit.*

*Und meinen Neffen Janosch*

# Acknowledgments

This PhD really resulted from a dream I had a while ago in Germany: After the “Census of Marine Life” project ended and it was time for me to finally start my PhD, I was determined to do it in Spain, and with cephalopods, ah, and preferably at the Mediterranean side, claro esta... Not everyone laughed at me, but most thought I am a bit crazy, leaving the stability of my home and go to a country deep in crisis, without any PhD in sight.

Wolle, my partner at that time, did not mind, gave up his good job and German life as well, and our adventure started, in Barcelona. Although it did not work out between us in the end, I will always be thankful to him for trying, and his company and support during this journey.

I am also thankful to Pedro Martinez, who agreed to my request to take with me the half-time position I had at Senckenberg and work remotely from Spain. The next personsto thank is Uwe Piatkowski for putting me in contact with Roger Villanueva. And of course Roger himself, who took me on at the CSIC Barcelona to make my first hands-on experience on cephalopod aquaculture and artificial fertilization. That was a great opportunity for me, and he also made me aware of the position opening up within the IEO, in Mallorca, on cephalopods!! Now, I did not want to be on this island with all the drunken German co-fellows, but in the end I did contact Toni Quetglas, the supervisor, and applied.

A few months later I started my new life in Mallorca, and have not regretted it since. Toni turned out to be one of these rare supervisors who really are present instead of travelling, and always there when you need their advice. His patient and very thorough way of correcting my first trials of scientific writing always impress me, and I am very thankful for all his effort, support and good humor. Thanks a lot Toni!! When it comes to modeling, I rely on the advice of Manolo Hidalgo, who is the co-supervisor of this thesis. It always amazes me how he copes with all his duties and still always finds time for others, while constantly keeping up this quiet, gentle good humor. So glad for your help and motivation! Many thanks to both of you with all my heart!

During the thesis, I spent 8 months abroad in different labs, first in France under the supervision of Jean-Paul Robin, who introduced me to stock assessment, and then in Sweden as guest of Valerio Bartolini, who showed a lot of patience teaching me R and modeling. Finally, Roger Hanlon agreed to host me at the MBL at Woods Hole. The first book on cephalopods that I read, before starting to work with them, was his, so it was quite special for me to be at his lab and learn from his huge experience. All of them were really friendly and committed hosts and took very good care of me. Thank you everyone! I really enjoyed my times there! And I also have to mention all the people who welcomed me and included me in their daily life and activities and made me feel welcome: Michael, George, Pauline, Marie and Martin in France, Francesca, Max, Kathi, Michele, Stefan and Jonathan in Sweden, and my housemate James for his generosity and caring in the US.

Three chapters of my thesis were based on data from MEDITS surveys, so my thanks to all crew and scientists in all countries. And to all my work colleagues, specially my office mate Alberto, for good talks and always helping me out when needed. And to Patri for all her help with my struggles with R. I will finish the “scientific part” thanking Graham Pierce for taking the time to motivate and help me after an unpleasant experience.

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## List of publications

This PhD thesis is structured as a compendium of the research articles listed below (published, in press or in preparation):

PART I:

1. Keller S., Hidalgo, M., Bitetto I, Casciaro L, Cuccu D, et al. In preparation. Demersal cephalopod communities in the Mediterranean – a large-scale analysis

2. Keller S, Bartolino V, Hidalgo M, Bitetto I, Casciaro L, Cuccu D, et al. 2016. Large-Scale Spatio-Temporal Patterns of Mediterranean Cephalopod Diversity. PLoS ONE 11(1): e0146469. doi:10.1371/journal.pone.0146469

Impact factor: 3.53

3. Keller S., Quetglas, A., Puerta, P., Bitetto I, Casciaro L, Cuccu D, et al. 2017. Accepted. Environmentally driven synchronies of Mediterranean cephalopod populations. Progress in Oceanography, in press

Impact factor: 3.51

PART II:

4. Keller, S., Valls, M., Hidalgo, M., Quetglas, A. 2014. Influence of environmental parameters on the life-history and population dynamics of cuttlefish *Sepia officinalis* in the western Mediterranean. Estuarine, Coastal and Shelf Science, 145, 31-40

Impact factor: 2.33

5. Keller, S, Robin, J.P., Valls, M., Gras, M. Cabanellas-Reboredo, M. and A. Quetglas. 2015. The use of Depletion Methods to assess Mediterranean cephalopod stocks under the current EU Data Collection Framework. Mediterranean Marine Science 16 (3), 513-523

Impact factor: 1.87

# Abstract

Cephalopods constitute an important faunistic group in marine ecosystems, representing keystone elements in marine food webs. Additionally, they are an important fishing resource, and their contribution to worldwide fishery landings has been rising significantly over the last decades. In the Mediterranean Sea, several local short-term studies on cephalopod abundance and distribution exist, but few integrate longer time scales and larger areas. The present thesis work combines large-scale, long-term studies on cephalopods community composition, diversity and abundance (Part I) with small-scale, local case studies around the Balearic Islands (Part II).

First, a community analysis was conducted at the whole Mediterranean scale in order to describe the present status and reveal possible differences between the western and the eastern Mediterranean sub-basins (Chapter 2). The aim was to compare assemblage structures between sub-basins together with the influence of large-scale environmental gradients on species composition. While basins did not differ significantly in cephalopod species composition, relative species contributions varied. Cephalopods are very sensitive to environmental changes, and adapt quickly due to their short life cycle and typically seasonal semelparity impeding generation buffering. Therefore sea surface temperature (SST) and chlorophyll *a* (Chl *a*) were hypothesised and documented as important drivers of cephalopod assemblages. While their importance differed between sub-basins, depth was confirmed as the most important factor structuring cephalopod communities.

At the same spatial scale, cephalopod diversity was analysed during two decades (Chapter 3). Results revealed the absence of clear longitudinal or latitudinal gradients in cephalopod diversity, combined with no distinct temporal trends over the last twenty years. Besides, temporal changes in diversity varied between various Mediterranean sub-regions. Location, depth, SST and productivity regime resulted to influence diversity.

To assess whether environmental variability impacts cephalopod populations at species level, the influence of SST and surface primary production on the spatial structuring and the population dynamics of two commercially important cephalopod species was investigated (Chapter 4). Although *Octopus vulgaris* and *Illex coindetii* exhibit contrasting life history traits and inhabit different habitats, long-term abundance trends and synchronic behaviour of their populations was similar, and population sub-structuring across the Mediterranean Sea were revealed. In consistency with former chapters, SST and Chl *a* regimes were shown to be significant drivers of distribution patterns and inter-annual abundance fluctuations.

The motivation for the second part of the thesis was fuelled by the present situation in the Mediterranean Sea, where cephalopod stocks are presumably overexploited, but where their ad-hoc assessment and management is far from being implemented. To contribute to existing knowledge of the current situation in the Balearic Sea, a case study on cuttlefish fishery, life-history and population dynamics was conducted using short-term and intra-annual data (Chapter 5). Possible drivers of cuttlefish abundance fluctuations were analysed, revealing significant influences of SST and local climatic variability. While the study provided an overview of possible intrinsic and extrinsic drivers of cuttlefish population fluctuations in the Balearic Sea, the next step was applying stock assessment techniques to cuttlefish and squid fisheries of this area (Chapter 6). Being the first application of depletion methods to Mediterranean cephalopod stocks, the study combined information of those two fisheries with the evaluation of this stock assessment method for short life cycle species. Results uncovered existing problems and suggested that the current sampling scheme under the EU-Data Collection Framework is inadequate for cephalopods in view of the assessment´s data requirements. Consequently, a modification of the existing scheme was proposed.

# Resumen

Los cefalópodos constituyen un grupo faunístico importante en los ecosistemas marinos, representando elementos clave en la estructura y dinámica de las redes tróficas. Además, son un importante recurso pesquero y su contribución a los desembarcos pesqueros mundiales se ha incrementado significativamente en las últimas décadas. En el Mar Mediterráneo existen varios estudios locales sobre la abundancia y distribución de cefalópodos, pero pocos integran escalas temporales largas y áreas extensas. Esta tesis combina estudios sobre la estructura de la comunidad, la diversidad y la abundancia de cefalópodos a gran escala espacio-temporal (Parte I) con estudios a escala local alrededor de las Islas Baleares (Parte II).

En primer lugar, se realizó un análisis de la comunidad de cefalópodos a escala de todo el Mediterráneo para describir el estado actual y determinar posibles diferencias entre las sub-cuencas occidental y oriental (Capítulo 2). El objetivo fue comparar la estructura de las comunidades faunísticas entre estas dos sub-cuencas y analizar la influencia de gradientes ambientales a gran escala sobre la composición específica. Aunque no se observaron diferencias significativas en la composición específica, las contribuciones relativas de las diferentes especies variaron entre ambas cuencas. Debido a su corto ciclo vital y estrategia reproductiva semélpara, los cefalópodos son muy sensibles a los cambios ambientales, adaptándose a ellos con relativa rapidez. Se esperaba, por tanto, que factores ambientales como la temperatura superficial del mar (SST) y el contenido de clorofila a (Chl *a*) fueran factores importantes en la estructuración de las comunidades de cefalópodos. Si bien su importancia difirió entre las dos sub-cuencas, se confirmó que la profundidad era el factor estructural más importante en dichas comunidades.

Se analizaron también cambios en la diversidad específica de las comunidades de cefalópodos a escala de todo el Mediterráneo durante los últimos 20 años (Capítulo 3). Los resultados no mostraron ninguna tendencia temporal ni espacial (latitud, longitud) clara y homogénea en la diversidad. Las únicas tendencias temporales observadas variaron entre diferentes sub-regiones, siendo la posición geográfica, profundidad, SST y productividad los principales factores determinantes de estas tendencias.

Para confirmar la importancia de la variabilidad ambiental a nivel específico, se analizó la influencia de la SST y la producción primaria en la estructura espacial y la dinámica poblacional de dos especies de cefalópodos de importancia comercial (Capítulo 4). Aunque *Octopus vulgaris* e *Illex coindetii* exhiben diferentes estrategias vitales y viven en diferentes hábitats, las tendencias temporales a largo plazo en su abundancia y el comportamiento sincrónico de sus poblaciones fueron similares, observándose sub-poblaciones temporalmente persistentes a lo largo de todo el Mediterráneo. En consonancia con los capítulos anteriores, la SST y Chla resultaron ser factores significativos en la definición de patrones de distribución y fluctuaciones interanuales de la abundancia.

La segunda parte de la tesis estaba motivada por la situación actual de los cefalópodos en el Mar Mediterráneo, donde no existen medidas de evaluación y gestión específica para este grupo y algunas de sus poblaciones se encuentran sobreexplotadas. Para contribuir al conocimiento de la situación actual en el Mar Balear, se analizó la pesquería, ciclo vital y dinámica poblacional de la sepia utilizando series temporales intra-anuales (Capítulo 5). El análisis de diferentes factores ambientales reveló que la SST y la variabilidad climática local influían significativamente en las fluctuaciones de abundancia de la especie. En un trabajo posterior (Capítulo 6) se aplicaron técnicas de evaluación de stocks a las pesquerías de sepia y calamar de las Islas Baleares utilizando datos procedentes de la *EU Data Collection Framework (DCF)*. Hasta donde sabemos, este trabajo constituye la primera aplicación de los *Lesly-Delury Depletion Methods* a stocks de cefalópodos del Mediterráneo. Los resultados demostraron que el esquema actual de muestreo de la DCF es inadecuado para la evaluación de cefalópodos y se proponen posibles modificaciones.

# Resum

Els cefalòpodes constitueixen un grup faunístic important als ecosistemes marins, essent elements clau a les xarxes tròfiques. A més, són importants recursos pesquers i la seva contribució als desembarcs pesquers mundials s'ha incrementat en les últimes dècades. representant al voltant del 30% de la captura desembarcada a nivell mundial. Al Mar Mediterrani existeixen varis estudis locals sobre l'abundància i distribució de cefalòpodes, però pocs integren escales temporals llargues i àrees extenses. Aquesta tesi combina estudis sobre la composició de la comunitat, la diversitat i l'abundància de cefalòpodes a gran escala espaciotemporal (Part I) amb estudis a escala local al voltant de les Illes Balears (Part II).

En primer lloc, es va realitzar un anàlisi de les comunitats de cefalòpodes a escala de tot el Mediterrani per descriure l'estat actual i determinar possibles diferències entre les sub-conques occidental i oriental (Capítol 2). L'objectiu fou comparar l'estructura de les comunitats faunístiques entre sub-conques i analitzar la influència de gradients ambientals a gran escala sobre la composició específica. Tot i que no s'observaren diferències significatives en la composició específica, les contribucions relatives de les diferents espècies variaren entre sub-conques. Degut al seu cicle vital curt i estratègia reproductiva semèlpara els cefalòpodes són molt sensibles als canvis ambientals, adaptant-se a ells amb relativa rapidesa. S'esperava, per tant, que factors ambientals com la temperatura superficial del mar (SST) i el contingut de clorofil·la a (Chla) fossin factors importants en l'estructuració de les comunitats de cefalòpodes. Si bé la seva importància va diferir entres les dues sub-conques, es va confirmar que la profunditat era el factor estructural més important en aquestes comunitats.

S'analitzaren també canvies en la diversitat específica de les comunitats de cefalòpodes a escala de tot el Mediterrani durant els últims 20 anys (Capítol 3). Els resultats no mostraren cap tendència temporal ni espacial (latitud, longitud) clara i homogènia en la diversitat. Les úniques tendències temporals observades variaren entre diferents sub-regions, essent la posició geogràfica, profunditat, SST i productivitat els principals factors determinants d'aquestes tendències.

Per tal de confirmar la importància de la variabilitat ambiental a nivell específic, es va investigar la influència de la SST i la producció primària en l'estructuració espacial i la dinàmica poblacional de dues espècies de cefalòpodes d'importància comercial (Capítol 4). Tot i que *Octopus vulgaris* i *Illex coindetii* tenen característiques vitals diferents i viuen en hàbitats diferents, les tendències temporals a llarg plaç en la seva l'abundància i el comportament sincrònic de les seves poblacions va ser similar, observant-se sub-poblacions temporalment persistents al llarg del Mediterrani. En consonància amb els capítols anteriors, la SST i Chla resultaren ser factors significatius en la definició de patrons de distribució i fluctuacions interanuals de l'abundància.

La segona part de la tesi estava motivada per la situació actual dels cefalòpodes al Mar Mediterrani, on no existeixen mesures d'avaluació i gestió específica per aquest grup i algunes de les seves poblacions es troben sobre-explotades. Per contribuir al coneixement de la situació actual al Mar Balear, es va analitzar la pesqueria, cicle vital i dinàmica poblacional de la sípia utilitzant sèries temporals intra-anuals (Capítol 5). L'anàlisi de diferents factors ambientals va revelar que la SST i la variabilitat climàtica local influïen significativament en les fluctuacions d'abundància de l'espècie. En un treball posterior (Capítol 6) s'aplicaren tècniques d'avaluació d'stocks a les pesqueries de sípia i calamar de les Illes Balears utilitzant dades procedents de la *EU Data Collection Framework (DCF).* Fins on sabem, aquest treball constitueix la primera aplicació dels *Lesly-Delury Depletion Methods* a stocks de cefalòpodes del Mediterrani. Els resultats demostraren que l'esquema actual de mostratge de la DCF és inadequat per a l'avaluació de cefalòpodes i es proposen possibles modificacions.

# Acronyms and abbreviations

| | |
|---|---|
| AIC | Akaike Information Criterion |
| AICc | Corrected Akaike Information Criterion |
| ANCOVA | Analysis of Covariance |
| AW | Atlantic Water |
| BTF | Bottom Trawl Fishery |
| CEDA | Catch and Effort Data Analysis |
| CFP | Common Fisheries Policy |
| Chla | Chlorophyll a |
| CPUE | Catch Per Unit Effort |
| DCF | Data Collection Framework |
| DFA | Dynamic Factor Analysis |
| DGW | Digestive Gland Weight |
| DM | Depletion Methods |
| EAF(M) | Ecosystem Approach to Fisheries (Management) |
| EMI | Emptiness Index |
| ENSO | El Niño Southern Oscillation |
| EW | Eviscerated Weight |
| FAO | Food and Agriculture Organization of the United Nations |
| GAM | General Additive Model |
| GCV | Generalized Cross-Validation Criterion |
| GFCM | General Fisheries Commission for the Mediterranean |
| GLM | General Lineal Model |
| GSA | Geographical Sub-Area |
| GSI | Gonadosomatic Index |
| GW | Gonad Weight |
| H’ | Shannon-Wiener Diversity |

| | |
|---|---|
| ICES | International Council for the Exploration of the Sea |
| IPCC | Intergovernmental Panel on Climate Change |
| LCI | Local Climatic Index |
| LIW | Levantine Intermediate Water |
| MAW | Modified Atlantic Water |
| MDR | Minimum Data Requirement |
| MEDITS | Mediterranean International Trawl Survey |
| ML | Mantle Length |
| MODIS | Moderate Resolution Imaging Spectroradiometer |
| MOI | Mediterranean Oscillation Index |
| MSFD | Marine Strategy Framework Directive |
| NAO | Northern Atlantic Oscillation |
| NEA-WC | North East Atlantic and Western Channel |
| RC | Reproductive Condition |
| S | Species richness |
| SC | Somatic Condition |
| SeaWiFS | Sea-viewing Wide Field-of-view Sensor |
| SSF | Small-Scale Fishery |
| SST | Sea Surface Temperature |
| TW | Total Weight |
| VIF | Variance Inflation Factor |
| WeMO | Western Mediterranean Oscillation |
| WIW | Western Intermediate Water |

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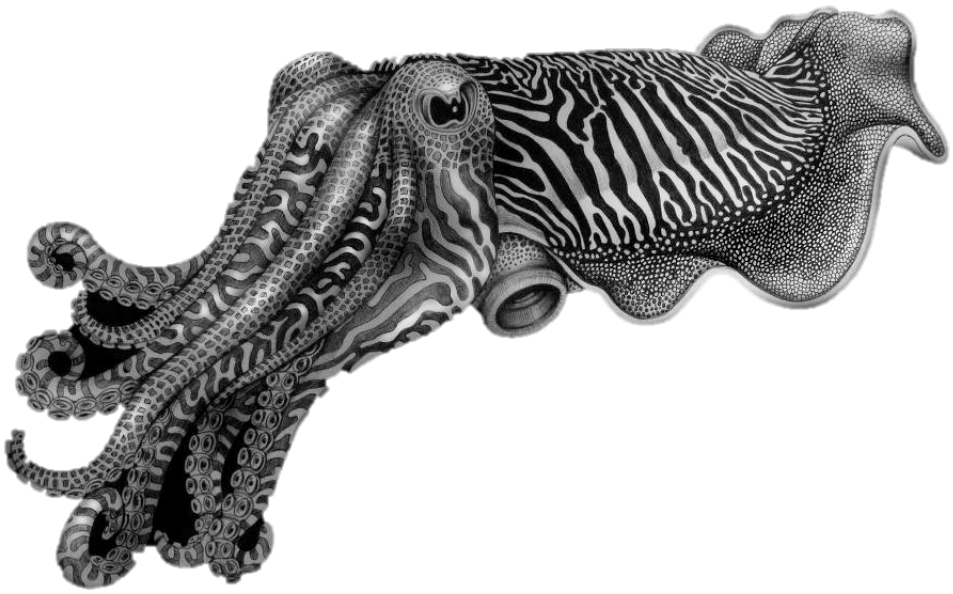


# Introduction

# Introduction

## 1.1 General introduction

### 1.1.1 Thesis motivation and aims

Basic knowledge on marine species diversity, community composition and population dynamics is important for ecosystem conservation and management, and therefore affects different sectors from local fisheries to regional planning to national and international environmental politics. While much is known about fish, cephalopods are less studied, even despite their important role in the food web of marine ecosystems (Hunsicker et al., 2010; Coll et al., 2013) and in fisheries worldwide (FAO, 2016). Various reasons are responsible for this under-representation. On one hand, their life-history traits differ significantly from fish, and therefore require the modification of some of the usual analytical assessments and management tools (Pauly, 1985; Pierce and Guerra, 1994). On the other hand, their distribution is very patchy, their generation times are short, the aging of species is tedious and their cultivation is difficult, to name but a few obstacles cephalopod scientist encounter. Most of the field studies available nowadays are based on fishery data, with the consequence that non-commercial species are much less studied (Quetglas et al., 2005).

Cephalopods show increasing abundances in many regions around the world (Doubleday et al., 2016). This increase, and also their rising importance as food resource, has been reason for many speculations and studies about the underlying causes (Balguerías, 2000; Vecchione et al., 2009; Doubleday et al., 2016). In complex ecosystems like the marine one, determining and disentangling influencing factors is less than trivial, but each study contributes valuable knowledge towards the functioning of our seas. The bigger part of existing cephalopod studies has been conducted in the Atlantic and Pacific Oceans. As explained in the section "Study area" below, our area of interest, the Mediterranean Sea, is different from these seas since it is influenced by regimes and mechanisms that vary from the rest of the world's oceans (Bas, 2009; Lejeusne et al., 2010). Existing cephalopod studies in this sea are usually of short time frames and on a rather local spatial scale.

One aim of the present thesis is to provide important and needed knowledge of Mediterranean cephalopod population dynamics and diversity patterns at several spatial and temporal scales, using information of the last 20 years. The first part of this thesis has a broad focus on regional patterns and includes long-term Mediterranean-scale analyses regarding community composition, species diversity and population dynamics. The second part comprises two local short-term case studies from the Balearic Islands (Western Mediterranean): the first one investigates environmental influences on the Majorcan cuttlefish fishery and the second tests the applicability of stock assessment tools on loliginid squid and cuttlefish. Each part will be introduced in detail in separate sections below.

The present work constitutes a valuable contribution to current knowledge on cephalopods for two reasons: First, the spatial extension of some studies includes the whole longitudinal gradient of the Mediterranean Sea and gives unique opportunities to

compare regions of different temperatures and productivity regimes. To our knowledge, no former cephalopod studies exist covering this entire sea. Second, this work is based on time series of up to 20 years. In the Mediterranean, analysis of similar time frames are very rare, despite the fact that the study of cephalopod population dynamics implies the necessity of long-term studies for two reasons: the typically very variable dynamic of cephalopod populations, and the underlying important ecological processes at play, which can often only be investigated at long temporal scale.

This thesis not only supplies a description of present and past status and trends, but also investigates plausible causes of the spatio-temporal patterns observed. To this goal, analysed drivers include environmental factors as well as habitat heterogeneity. This way, the thesis will provide important insight needed to implement the ecosystem approach to fisheries (EAFM), which nowadays is considered the adequate framework to conduct integrative and effective fisheries management (Hilborn, 2004; Pikitch et al., 2004).

### 1.1.2 Structure of the thesis

The thesis consists of two main sections: The first part (Chapters 2 - 4) has a broader focus and treats large-scale spatio-temporal patterns at the scale of the entire Mediterranean Sea, while the second section (Chapters 5 - 6) focuses on a much smaller scale, investigating intra-annual processes and patterns on a local geographic scale. The first three chapters (Section 1) investigate the composition of the cephalopod community (Chapter 2), their diversity over time and space (Chapter 3), and the population dynamics of two commercial species (Chapter 4). The aim of this section is to reveal important biogeographical patterns and the forcing drivers that help us to understand the spatio-temporal dynamics and distribution of cephalopods within the entire Mediterranean Sea.

The second section (Chapters 5 - 6) focuses on the Balearic Sea. The conducted studies take place at the inter-annual scale of months and are of regional importance to the fisheries management of the Balearic Islands. In chapter 5, the local cuttlefish fishery (which is the main small-scale cephalopod fishery in the Balearic Islands) is described and drivers of observed patterns are investigated. Furthermore, some life-history aspects of *S. officinalis* are examined. In chapter 6, a case study using the Leslie-Delury stock assessment method (DeLury, 1947; Leslie and Davis, 1939) assesses the suitability of depletion-based cephalopod assessment and existing sampling scheme set up by the European commission.

### 1.1.3 The study subjects: Cephalopods

Cephalopods are one class of the phylum mollusca and include about 800 known living species belonging to the subclasses nautiloidea (nautilus) and coleoidea (octopus, cuttlefish and squid). They can be found in all the world's oceans, with the exception of sepiidae (cuttlefish) in the Americas. Cephalopods are characterized by quite diverse life-history strategies and habitats, and species are found from the shallow waters to the open ocean and also in the deep sea, inhabiting benthic, necto-benthic or pelagic habitats. While octopuses are mostly solitary, others form schools (squid) or at least spawning

aggregations (cuttlefish). Loliginid squids, cuttlefish and octopus usually conduct spawning migrations towards shallower coastal waters for reproduction, and attach their eggs to hard substrates (cuttlefish, loliginids) or inside dens (octopus). While cuttlefish and squids do not provide any further parental care to their eggs, female octopuses stay with their eggs until hatching, supplying them with aerated water and defending them. Open ocean squids, on the other hand, produce eggs of neutrally buoyancy bundled together in free floating gelatinous egg masses (Boyle and Rodhouse, 2005). While only squid and octopus have paralarvae (early life stage after hatching characterised by a planktonic phase), all early life stages of cephalopods are especially sensitive to environmental influences and predation. The first weeks to months therefore constitute a critical phase in the cephalopods life cycle, where outer influences are important determinates of growth and mortality, impacting subsequent life stages and partially determining population fluctuations.

Cephalopods have very different life history characteristics from fishes. For example, they usually have short life spans (1-2 years), exhibit fast growth rates, show high plasticity of their life-history traits and many species conduct spawning and reproductive migrations to shallower waters. In general, cephalopods are semelparous, that is they breed only once at the end of their life cycle (Boyle and Rodhouse, 2005). This latter characteristic is responsible for very little generation overlap, which makes the population of one year very dependent on the reproductive success of the previous generation and the survival rate of the new recruits. In other words, populations re-new themselves from generation to generation (i.e. from year to year), and high variability in yearly abundances are therefore a typical characteristic of cephalopod populations. Their short live cycle and the little or no existent generation overlap also allows a quick adaptation of populations to environmental changes (Pierce et al., 2008). Together with their sensitivity for external influences and their high plasticity, this characteristic potentially makes cephalopods a good indicator for ecosystem changes (Tian, 2009).

The study of cephalopods is important for various reasons. First, they are increasingly important as fishery resource in many countries, were they generate employment and are a healthy food source rich in proteins and poor in fat. Depletion of fish stocks or other changes in ecosystems, market demand and fishing technologies have led to increasing landings in the last decades (Caddy and Rodhouse, 1998; Doubleday et al., 2016), with annual amounts around 4 million tons (Stergiou et al., 2006; FAO, 2016). Overfished finfish stocks result in released predation and competition pressure on cephalopods, which may have also taken advantage of vacant ecological niches left by finfishes (Caddy and Rodhouse, 1998; Vecchione et al., 2009, Balguerías, 2000).

Apart from being a fishery resource, cephalopods play an important role in marine ecosystems. They are a food source for many predators and, on the other hand, are voracious predators themselves, influencing food webs substantially (Coll et al., 2013; Navarro et al., 2013). They are opportunistic species feeding on crustaceans, molluscs, fishes and also on other cephalopods including their own species. They are important for the energy transfer within trophic webs (André et al., 2010) and their high growth rates require high consumption rates, causing significant effects on their prey populations. On the other hand, cephalopods are themselves preyed by upper trophic levels such as large oceanic fish (e.g. sharks, tuna, and swordfish) (Smale, 1996), marine mammals like

dolphins and whales (Clarke, 1996; Klages, 1996), and also big marine birds like albatrosses (Croxall and Prince, 1996).

Case study species

Some chapters of this thesis focus on single species, namely on *Octopus vulgaris*, *Illex coindetii, Sepia officinalis* and *Loligo vulgaris*. Therefore, a short description including the biology, life-history and fishery of each species will be given below.

The common cuttlefish *Sepia officinalis* Linnaeus, 1758 is a semelparous, nekto-benthic species exhibiting a short life-cycle of 1-2 years. Big animals can reach a mantle length of about 45 cm and a weight of 4 kg, mainly preying on small molluscs, crabs, shrimps and some fish. Their predators are sharks, fish and other cuttlefish. Their usual habitat is sandy to muddy bottom no deeper than 150 m. The species can be found all along the Mediterranean Sea and in the eastern Atlantic from Northern England down to the northwest coast of Africa. Most studies regarding its fishery originate from the Atlantic or English Channel (e.g. Boletzky, 1983; Gauvrit et al., 1997; Denis and Robin, 2001; Wang et al., 2003; Royer et al., 2006). Around Mallorca, these cuttlefish undergo important spawning migrations to the coast between February and May, where they mate and attach their eggs to hard substrates in shallow water. The species constitutes a valuable fishing resource, and it is during this reproduction season when the artisanal fishery catches them in large numbers with trammel nets (Merino et al., 2008; Quetglas et al., 2016; Chapter 5 of this thesis), while all year around, in much less numbers, they are also caught by bottom trawlers within their multi-species fishery activities (Quetglas et al., 2000, Chapter 6).

The European squid, *Loligo vulgaris* Lamarck, 1798, can reach a maximum mantle length of about 42 cm (32 in females) and a maximum weight of 1.5 kg. The neritic, semi-demersal species prefers shallow water and occurs to a maximum of about 500 m, with a peak between 20 and 250 m. The squid has been found in the Eastern Atlantic from the North Sea down to the west coast of Africa (Gulf of Guinea) (Worms, 1983; Guerra and Rocha, 1994). It conducts feeding and spawning migration to shallower waters (normally in spring), where it attaches its eggs in gelatinous

tubes to solid objects over sandy or muddy bottom. Males grow faster than females and reach bigger sizes (Arkhipkin, 1995). Around Mallorca, this species is fished by recreational fishermen and as bycatch by the commercial trawling fleet (Morales-Nin et al., 2005).

The broadtail shortfin squid *Illex coindetii* (Veranyi, 1839) is an oceanic, nekto-benthic species which can reach about 38 cm. The species occurs between 50 and 1100 m, but highest abundances are usually found between 50 and 100 and 400 to 600 m (Roper et al., 2010). The distribution of *I. coindetii* includes both sides of the Atlantic Ocean, from Ireland down to Namibia in the east and down to the Caribbean Sea on the western Atlantic side. These squids are often found on the sea floor during the day, while it ascends towards the surface at night to feed (Roper et al., 2010). Seasonal migration between deeper and shallower water have been observed and take place between spring and autumn in the Mediterranean, depending on the area. Eggs are laid in gelatinous, free floating egg masses. Typical preys of the squid are pelagic crustaceans, fish and other cephalopods, while whales and fish are its main predators (Roper et al., 2010). *I. coindetii* is fished as bycatch by the commercial trawlers in the Balearic Sea.

The common Octopus, *Octopus vulgaris* Cuvier 1797, is a solitary, benthic species occurring in shallow water to a maximum of about 200 m (Belcari et al., 2002a). Highest abundances are found much shallower though, between 25 and 50 m (Silva et al., 2002). Preferred substrate consists of rocky bottom or coral reefs, as the animal uses caves of rocks or reefs as dens. It can grow to about 25 cm of mantle length and reach a diameter of over 1 m including its arms (Norman, 2000). Its distribution is worldwide in tropical and temperate waters. The life span of this species is 11 - 15 months (Katsanevakis and Verriopoulos, 2006), and the eggs (which the female attaches to the ceiling of her den) are brooded until hatching. Hatched paralarvae undergo a planktonic life phase of probably about 40 - 60 days before they settle to the seafloor and become benthic (Villanueva, 1995). The species is mainly active between dusk and down. The prey of this octopus consists primarily of crustaceans and mollusc, while they serve as prey for larger fish and seals. Regarding fishery, the species is of considerable importance in fisheries around the world and is mainly fished with trawls and octopus pots (FAO,

2016). Around the Balearic Islands, together with *Eledone cirrhosa*, the octopus represents 20 – 40% of the total commercial fishery catches from the bottom trawl fishery (Quetglas et al., 1998).

Figure 1.1: Sampling cephalopods during the Spanish MEDITS survey around Mallorca.

## 1.2 PART I: Mediterranean-wide spatio-temporal analysis of cephalopod assemblages, diversity and population dynamics

### 1.2.1 Introduction to the topic

Why do we care?

Species composition and diversity have strong implications on the functioning and conservation state of ecosystems, and preserving this diversity should therefore be a priority in conservation management. This, in turn, requires the understanding of the causes of underlying distribution and abundance patterns and their interference with environmental conditions. The first step is therefore to analyse the present species composition in a given ecosystem and investigate possible drivers for the observed status (Chapter 2). Furthermore, diversity patterns and their changes with time are important information when it comes to understand our seas (Chapter 3). Where and why diversity hotspots can be found is indeed one of the most important questions for conservation purposes. The underlying causes are important to consider if we want to make predictions about future scenarios under climate change, different fishery pressures, growing human influences, etc. The same knowledge is crucial to prevent the decline of the current diversity and protect it more efficiently. For this, connectivity and synchrony between populations have to be considered as well, as they are fundamental for the dynamics of the system. While open populations with larval exchange are more resistant (able to withstand local disturbances) and recover quicker (higher resilience), populations fluctuating in synchrony due to external influences run a greater risk of extinction (Descamps et al., 2013). To break down these underlying processes, a complementary analysis of cephalopod population dynamics throughout the entire Mediterranean Sea was conducted (Chapter 4).

Diversity, connectivity and dynamics of marine populations are relevant issues for policy makers, who need to base their decisions regarding ecosystem conservation and fisheries management on sound scientific knowledge. In practice, the outcomes of the above studies shall be specifically useful in the context of the regionalization objectives under the current Common Fisheries Policy (CFP; EU Regulation Nº 1380/2013). At present, the ongoing regionalization approach is considering the management units currently in place in the Mediterranean Sea, revising possible alternatives and re-organization. To find an ecologically meaningful solution, we need to know which mechanisms control stock limits and fluctuations. Otherwise, the risk of merging independently fluctuating populations to a common management area increases and may result in strong miss-management.

What is known?

In the Mediterranean, broad-scale analyses directed to the above purposes are scarce, and mainly exist for fish (Gaertner et al., 2007, 2013; Granger et al., 2015) and overall biodiversity (Coll et al., 2010, 2012; Danovaro et al., 2010). These studies are generally descriptive and comparative and do not explicitly include underlying drivers of observed patterns other than depth. At smaller scale, however, temperature, chlorophyll a content, prey availability and climatic phenomena have been shown to provide important

insights to understand existing species distributions and dynamics (González and Sánchez, 2002; Keller et al., 2014 / Chapter 5; Navarro et al., 2016; Pierce et al., 2008; Puerta et al., 2015, 2014). Therefore, when possible, information of the most relevant drivers should be included in large-scale studies.

To assess the influence of environmental variability at large scales, it is crucial to understand the spatial structure of populations and communities. Studies on spatial synchrony can indirectly provide this information, as - apart from influencing abundances and distribution - environmental and large-scale climatic variability can force spatially distant populations to fluctuate in synchrony (Liebhold et al., 2004). Although this has already been described on a large scale for fish (Kelly et al., 2009), crustaceans (Koeller et al., 2009; Hidalgo et al., 2015) and plankton (Doyle and Poore, 1974; Batchelder et al., 2012), currently just a single local study about seasonal synchronies exists for cephalopods (Puerta et al., 2016b).

What can this thesis contribute?

The thesis intents to broaden our understanding of diversity, community structure and population dynamics of cephalopods at the biogeographical scale of the Mediterranean Sea. The current lack of large-scale, long term cephalopod studies and missing information about underlying mechanisms was one of the motivations of the present thesis. The work presented in the different chapters of this section reveals underlying mechanisms that shall be useful to include in fishery stock assessment.

The community analysis in chapter 2 gives an overview of the existing demersal cephalopod species in the Mediterranean and observed community compositions of both eastern and western basin. Structuring factors like depth, location, temperature, and productivity regime are analysed and compared between basins. For this analysis we use an innovative approach of combining non-dimensional scaling with general additive models (GAMs). In the marine environment, this technique has been used with fish and larvae data (Siddon et al., 2011; Hidalgo et al., 2014) and constitutes a useful alternative to more common multivariate analysis. Putative drivers can be integrated directly, and this way, further knowledge is gained beyond the mere splitting into different communities.

Chapter 3 deals with spatio-temporal diversity patterns of Mediterranean cephalopods. First, an explorative data analysis is carried out, comparing α - and ɣ - diversity of six different Mediterranean sub-regions using species richness and the Shannon-Wiener index as diversity measurements. Temporal diversity patterns over the last two decades are analyses at regional and sub-regional levels, and GAMs are applied to detect underlying influences of environmental variability on the observed patterns.

Chapter 4 analyses the population dynamics of two cephalopod species with contrasting life histories (*Illex coindetii* and *Octopus vulgaris*) over the last 20 years at regional scale of the entire Mediterranean. Synchronies in spatially distant populations were investigated using decorrelation techniques, and a dynamic factor analysis (DFA) is conducted to detect underlying common abundance trends over distant regions. Furthermore, putative influences of key environmental drivers such as productivity and sea surface temperature are analysed applying general linear models (GLM).

The data analysed in these chapters originate from a scientific research program carried out by (nowadays) all riparian EU countries during the last 20 years. Therefore, they have the advantage of being based on standardized methodology, making them comparable between locations. Furthermore, the input data is not biased by unreported catches, lost bycatch or preferences regarding any target species or fishing ground. These facts supply a unique opportunity for Mediterranean-wide comparisons without encountering the typical problems of fishery data or multiple studies from different surveys.

### 1.2.2 Study area: Mediterranean Sea

Figure 1.2: The Mediterranean Sea and the 21 countries surrounding it.

The Mediterranean Sea comprises about 2.9 Million km$^2$ and reaches a maximum depth of ~ 5.200 m, which makes it the largest semi-enclosed sea on our planet. It is surrounded by 21 countries which intensively use it for fishing, recreational and transportation purposes. In the west, the Sea is connected to the Atlantic Ocean via the 22 km wide Strait of Gibraltar, while in the north-east it has a natural connection with the Black Sea. On the other hand, the Suez channel to the Red Sea is man-made and facilitates the invasion of non-native species from this sea to the Mediterranean, causing one of today's ecological problems (Bas, 2009). The sea is divided into a western (area = 0.85 million km$^2$) and a wider eastern (area = 1.65 million km$^2$) basin by the Strait of Sicily, where the maximum depth between Europe and the African continent is 400 m. The Strait therefore constitutes a natural barrier for certain species and influences water exchange between basins.

The Mediterranean is a concentration basin, meaning that evaporation is higher than freshwater income via rivers and rainfalls, so the deficit is covered by the incoming Atlantic water. This water enters the Mediterranean as surface water (Atlantic Water – AW) and travels all the way eastwards, where it gets warmer and saltier and becomes Modified Atlantic Water (MAW). It finally sinks to deeper strata in the Levantine basin. Denser Mediterranean water creates a contra-current to the inflowing Atlantic water when it leaves Gibraltar close to the sea floor. Some special features of the sea are narrow continental shelves and stable temperatures from about 300-500 m depth on, with deep waters of unusually high temperature (about 13-15 ºC) and high salinity (37.5-39.5 psu).

Large scale gradients of temperature, productivity and salinity (D'Ortenzio and d'Alcalá, 2009) shape the sea, and local current regimes, river inputs, human influences and upwelling areas locally disrupt these patterns and add to the complexity of the system. Seafloor topography and hydrography are very variable as well (Millot, 2005; Rossi et al., 2014). Temperature increases from west to east, while the productivity gradient shows the opposite pattern. Sea surface temperature range between 12 and 27 ºC and shows marked seasonality, which is also true for the productivity regime. Even though Mediterranean waters are rather oligotrophic, the sea is considered a hotspot of marine diversity (Bianchi and Morri, 2000; Coll et al., 2010). Most species origin from the Atlantic Ocean, but high endemism can be found, too (Tortonese 1985). Although it makes up only 0.8% of the total world oceans, it comprises between 4 – 16 % of the estimated marine species, with about 25% of the fauna and flora being endemic (Bianchi and Morri, 2000). Regarding cephalopods, until date the occurrence of 66 species is confirmed (Bello, 2008).

### 1.2.3 Data source: MEDITS survey data

Data for Chapters 2 to 4 were obtained from the international Mediterranean bottom trawl survey MEDITS. This survey takes place on the continental shelves and along the upper and middle slopes of the Mediterranean Sea, and aims to obtain basic information on demersal species in terms of population distribution as well as demographic structure (http://www.sibm.it/MEDITS%202011/principalemedits.htm). The survey, which started in 1994 as a cooperation between Spain, France, Italy and Greece, is nowadays performed by all ten riparian EU countries in addition to Montenegro and Albania. Actually, since 2002, all European countries with Mediterranean coast have to conduct the survey annually as part of the European Data Collection Framework (DCF). Since then, funding is provided by the Directorate General for Maritime Affairs and Fisheries (DG-MARE) of the European Union and the national governments of each participating country. All data are submitted to the Joint Research Centre (JRC) in Varese, Italy, and are available to all EU member countries on demand. A specific MEDITS steering committee and working group meets annually and ensures consistency and coherence of the MEDITS surveys in space and time, reviewing standards and methodology regularly. They also coordinate data exchange within the group and resulting publications.

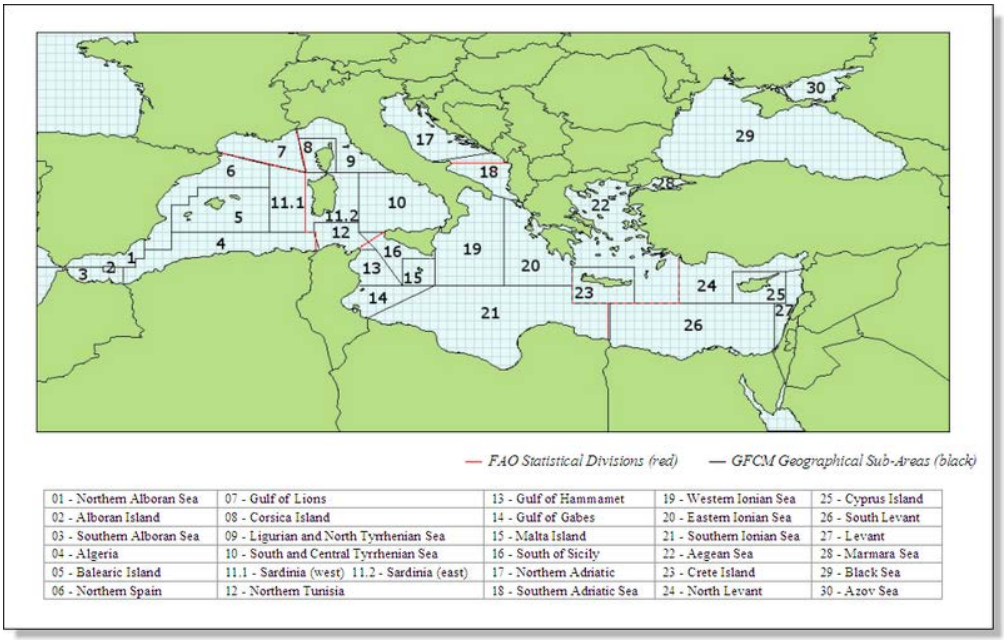
The survey gear, sampling protocol and methodology are standardized among all countries (for details see Bertrand et al., 2002 and A.A.V.V., 2016). Standardization includes the survey design, the sampling gear (feature and handling), the information collected and the management of the data including the production of common standardized analysis. The protocols are subject to constant revision during the annual meetings of the MEDITS group. Surveys are conducted every year in spring / summer (May-August), covering depths from 10 m down to 800 m. A stratified random sampling design is used, with bathymetric strata comprising 10-50, 51-100, 101-200, 201-500 and 501-800 m. The number of stations per stratum is proportional to its area, and whenever possible each station is to be held constant from year to year. On average, one station per 60 square nautical miles is intended, except in the Adriatic see where the rate is about every 200 square miles due to geographic differences. In the last years, about 1100 hauls are carried out annually throughout the Mediterranean by the MEDITS programme. Sampling takes place between half an hour after sunrise and half an hour before sunset, at

a speed of 3 knots and preferable at constant depth. Towing time is 30 minutes below 200 m and 60 minutes for deeper stations. More technical details can be found in the respective chapters of the thesis.

Figure 1.3: Research vessel Miguel Oliver used for the Spanish MEDITS surveys since 2014 (above) and different cephalopod species caught at a station around Mallorca (below).

Haul catches are sorted to species level whenever possible. Total weight and number are recorded for each species. For most fish species and certain other target species, length, sex and maturity are measured / determined as well, following the maturity protocols compiled by the MEDITS program. Abundance data for each species are standardized to number of individuals per $km^2$ using the mean stratified swept area method (Saville, 1977; Souplet, 1996).

Spatial sampling units are the geographical sub-areas (GSA's) established by the General Fisheries Commission for the Mediterranean (http://www.fao.org/gfcm/en/) for assessment and management purposes (Fig 1.2). By now, 18 GSAs of the 30 existing sub-areas take part in the program, which therefore constitutes the most comprehensive data source to investigate demersal ecosystems in the Mediterranean up to date. It supplies fishery-independent, long-term evaluation of demersal resources, including their abundance, distribution and population structure.




| | | | | |
|---|---|---|---|---|
| 01 - Northern Alboran Sea | 07 - Gulf of Lions | 13 - Gulf of Hammamet | 19 - Western Ionian Sea | 25 - Cyprus Island |
| 02 - Alboran Island | 08 - Corsica Island | 14 - Gulf of Gabes | 20 - Eastern Ionian Sea | 26 - South Levant |
| 03 - Southern Alboran Sea | 09 - Ligurian and North Tyrrhenian Sea | 15 - Malta Island | 21 - Southern Ionian Sea | 27 - Levant |
| 04 - Algeria | 10 - South and Central Tyrrhenian Sea | 16 - South of Sicily | 22 - Aegean Sea | 28 - Marmara Sea |
| 05 - Balearic Island | 11.1 - Sardinia (west) 11.2 - Sardinia (east) | 17 - Northern Adriatic | 23 - Crete Island | 29 - Black Sea |
| 06 - Northern Spain | 12 - Northern Tunisia | 18 - Southern Adriatic Sea | 24 - North Levant | 30 - Azov Sea |

Figure 1.4: Geographical sub-areas 1 – 30 set up by the General Fisheries Commission for the Mediterranean. Source: FAO / GCFM 2009, http://www.fao.org/gfcm/data/map-geographical-subareas/en/

Figure 1.5: Sampling during the Spanish MEDITS aboard RV Cornide de Saavedra.

## 1.3 PART II: Local cephalopod fisheries in the Balearic Islands

### 1.3.1 Introduction to the topic

Why do we care?

Traditionally, cephalopods are main fishing targets for Mediterranean countries. Especially *Sepia officinalis* and *Loligo vulgaris* are two economically important species for the whole Mediterranean region. Around the Balearic Islands, they support an artisanal (cuttlefish) and recreational fishery (squid) as well as being bycatch species with commercial value in the multispecies bottom trawl fishery. On the other hand, as most cephalopods, these species constitute important links in the energy transfer between trophic levels, and are therefore relevant for the functioning of the surrounding ecosystem. Proper assessment and management is therefore important to protect these species and maintain a sustainable fishing resource. To achieve this, detailed information about their life cycle, population structure and dynamics is essential. For short-living animals like cephalopods, the assessment improves from using data at intra-annual scale. Population dynamics of these animals are often connected to environmental influences (Pierce et al., 2008; Puerta et al., 2016b), wherefore additional knowledge about these mechanisms is of equal importance for fishermen and fishery managers.

Once sound scientific knowledge of the local populations is gained, only suitable and realistic assessment methods (and the thorough application of them) will enable decision makers to reach the goal of sustainable exploitation. Due to their different life history compared to fish, stock assessment of cephalopods requires ad-hoc methods (Pierce and Guerra, 1994). Current assessment methods used for fish often require generation overlap, knowledge about the age structure of the population, stock-recruitment relationships and closed populations without migration, facts often not given or hard to obtain in cephalopod populations. Furthermore, cephalopod fisheries are data-poor in many regions and therefore hard to analyse. To improve this situation, it is important to assess existing methods and their applicability in a specific area, as we do in the Balearic case study. This way, the usefulness of specific methods and the available data quality may be evaluated.

What is known?

Around the Balearic Islands, *S. officinalis* is a valuable fishery resource, with a seasonal small-scale fishery depending completely on the cuttlefish's yearly recruitment success (Quetglas et al., 2016). Knowledge of their population dynamics and underlying causes is therefore critical, but no studies exist in this area. Most cuttlefish studies have been conducted in the northeast Atlantic Ocean, where cephalopod life cycles, environment and fishing methods are rather different from the Mediterranean (e.g. Denis and Robin, 2001; Royer et al., 2006; Wang et al., 2003). In the Mediterranean, few studies analyse the exploitation patterns of this species (Belcari et al., 2002b; Merino et al., 2008) or their population dynamics, reproduction and ecology (but see Mangold-Wirz, 1963 for a general review and Laptikhovsky et al., 2003 and Onsoy and Salman, 2005 for reproduction).

Regarding underlying factors influencing the cephalopod dynamics, most works have been done on squid populations. Some of these works consider climatic influences at large scale, such as the North Atlantic Oscillation (NAO) (Pierce and Boyle, 2003; Sims et al., 2001) or the El Niño Southern Oscillation (ENSO) (Waluda et al., 2006; Quetglas et al., 2013), also combined with a local climatic index (Puerta et al., 2014). Surface temperature, productivity regime, winds, river discharges or rainfall are other possible drivers that have been investigated in cephalopod studies (Lloret et al., 2001; Arvanitidis et al., 2002; Georgakarakos et al., 2002; Sobrino et al., 2002; Wang et al., 2003).

The motivation for the chapter on stock assessment resulted from the fact that to date, the Spanish squid and cuttlefish fishery in the Mediterranean is only regulated by some restrictions of fishing activities (overnight, weekends). The trammel net fishery is regulated by a minimum mesh size and a maximum length according to crew size (with a maximum of 5000 m for crew sizes bigger than two fishers) (Orden AAA/2794/2012 del Boletín Oficial del Estado español). These general measures are important but inflexible, and do not adapt to arising needs within fishing seasons. Therefore, it is reasonable to examine if real-time stock assessment could be a useful tool to fine-tune cephalopod fishery rapidly and directed. Various methods exist, but certainly the most applied ones are depletion methods, which have been used for one of the biggest cephalopod fishery worldwide, the fishery of *Illex argentinus* and *Loligo gahi* stocks around the Falklands (Beddington and Rosenberg, 1990; Agnew et al., 1998; Arkhipkin et al., 2013). More recently, also in Europe, Leslie-DeLury depletion methods were applied to cuttlefish and squid fisheries from the English Channel and northern Scottish waters (Dunn, 1999; Royer et al., 2002, 2006; Young et al., 2004; Challier et al., 2005b).

### What can this thesis contribute?

In chapter 5, we present the first study of Mediterranean cuttlefish stocks around the Balearic Islands, including their fishery and population dynamics based on fishery statistics and biological sampling. The obtained biological information is the first published for this area and may serve as a baseline for further monitoring of future population development. The study also supplies useful information about biological and fishery characteristics of importance for stock assessment and management. A small temporal resolution of data (monthly) was chosen to catch short-term processes. The integration of these processes is of importance for ad-hoc fishery management and short-term forecasts, and is lacking in the many long-term fishery studies based on inter-annual data (Roel and Butterworth, 2000; Laurans et al., 2002; Quetglas et al., 2013, 2015).

In line with this, chapter 6 describes a stock assessment methods based on monthly data, and is the first application of depletion methods to Mediterranean cephalopod stocks. The chapter reveals existing problems and suggests potential improvements of this stock assessment method. Furthermore, it critically reviews the usefulness of the current sampling schemes in view of the assessment´s data requirements. As a result, a modification of the existing sampling scheme is proposed in order to comply with the model's input data requirements.

Input data for the two chapters are based on daily fishery records from all fishing grounds around Mallorca. Together with the fact that bycatch and unreported catches are

negligible (due to the high value of the species and non-existing quota) for the studied species, the provided datasets allows testing certain methods and analyses.

### 1.3.2 Study area: Balearic Sea


Figure 1.6: The Mediterranean Sea and the Balearic Sea placed in the Western Mediterranean sub-basin.

The Balearic Islands are placed in the western Mediterranean Sea, between the Balearic sub-basin in the north-west and the Algerian one in the south-east (Fig 1.3). The southern coasts of the Islands are reached by anticyclonic eddies of incoming Atlantic water meandering from the Algerian current along the North African coast. The Mallorca channel between Ibiza and Mallorca and the Ibiza Channel between Ibiza and the Spanish mainland are important gateways for water exchange between the less saline, warmer waters of the Algerian sub-basin and the cooler, more saline waters of the Balearic basin. Generally, the Balearic Sea is mainly influenced by the Northern Current coming down the Spanish mainland coast in southward direction. This current mainly consists of Atlantic water and splits into two branches when it reaches the Ibiza channel. While part of the current continues further downwards, another part returns northwards and continues alongside the north-western coasts of Ibiza and Mallorca, now named Balearic current (Monserrat et al., 2008).

At intermediate depths, two water masses are found: The Levantine Intermediate Water (LIW) and the Western Intermediate Water (WIW). The latter is formed in winter

over the continental shelf and the slope, but only in years which are characterized by cold winters and therefore deep convection events in the Gulf of Lions and the Ligurian Sea. It is therefore not present every year. Its presence or absence triggers two contrasting oceanographic scenarios. When WIW is present, new Atlantic water from the south cannot proceed through the Ibiza channel in spring, and therefore finds its way around the south of Ibiza and Formentera forwards Mallorca (Balbín et al., 2014). The oceanic front separating new and old Atlantic water (from the north) is therefore located south or southeast of the Islands. By contrast, in years with no WIW formation during winter, the new Atlantic water can reach further north and is able to flow around Ibiza, crossing the Mallorca channel towards Cabrera. The oceanic front is now located further north (Balbín et al., 2014).

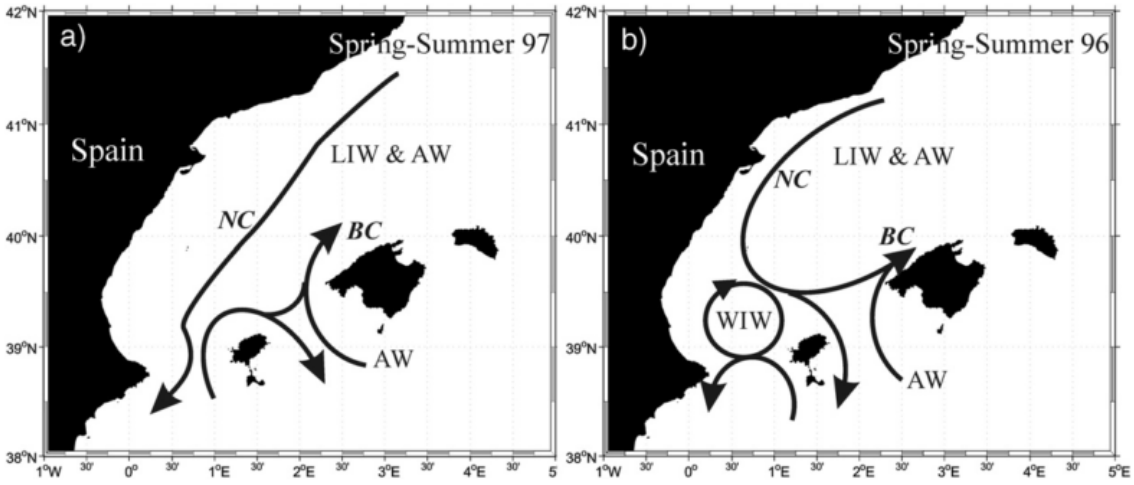



Figure 1.7: Scheme of the regional ocean circulation around the Balearic Islands after a relatively warm (a) and cold (b) winter. Major currents and water masses are indicated: the Northern Current (NC), the Balearic Current (BC), the LIW (Levantine Intermediate water, the AW (recent Atlantic water) and the WIW (Western Mediterranean Intermediate Water). Source: Monserrat et al. 2008.

Regarding geomorphology, the Balearic Sea can be distinguished from the Mediterranean waters around the Iberian Peninsula. The characteristics of the substrate around the islands are different, as it is dominated by bottoms of biogenic origin (Canals and Ballesteros, 1997), in contrast to the terrigenous sediments around the North West Iberian Peninsula. This causes a seabed composition different from the ones on the Mainland (Canals and Ballesteros, 1997; Acosta et al., 2002), which in turn leads to a different catch composition regarding the fishery (Carbonell et al., 1998; Sánchez et al., 2004). Fleet composition and importance of fishery type vary as well. In Mallorca, main fisheries constitute of the bottom trawl fishery (~70%), the small-scale fishery (~20%), the purse seine fishery (~10%) and the pelagic long line fishery, in the order of importance of their landings in kg (Quetglas et al., 2012, 2016). The island's fishing fleet is smaller compared to the mainland fleets, and the multispecies trawl fishery is of higher relative importance regarding its landings (70%, compared to 45-50%) (Quetglas et al., 2012). The islands small-scale fishery contributes around 16% to total landings, much more than on the mainland. Another difference is that over the shelf area around the

Archipelago, all demersal catches obtained can be identified, as no foreign fleets are fishing in this area (Quetglas et al., 2012).

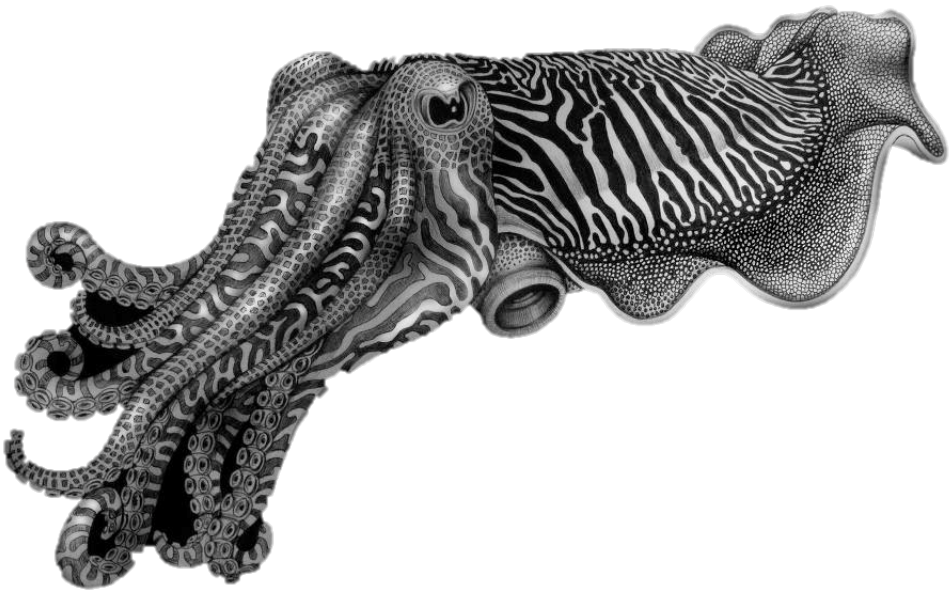
### 1.3.3 Data sources: Fishery data and biological sampling

For the assessment of cuttlefish and squid stocks, data were obtained from official fishery statistics (OP-Mallorcamar) of Mallorca (Balearic Islands). Since 2000, these data include the catches of all Majorcan fishing vessels on a daily basis. As discards of squid and cuttlefish are negligible in the area (Sartor et al., 1998), landings represent total declared catches, and catch per unit effort (CPUE) can be calculated by taking into consideration the fishing time or the horse power of each vessel. Around Mallorca, the duration of fishing activity is regulated by law to one day maximum, so all boats return to their home ports for the night.

Observer data were obtained by independent observers instated by the EU Data Collection Framework. Observers record the characteristics of each haul (location, depth, duration etc) and conduct size frequency sampling on board of commercial trawlers and artisanal fishing vessels.

Biological data (individual size and weight, eviscerated weight, sex, gonad weight, digestive gland weight and stomach weight) were obtained from monthly fish market samples analysed in the laboratory.


Figure 1.8: Observer sampling aboard an artisanal fishing boat.



# Chapter 2

# Demersal cephalopod communities in the Mediterranean

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## a large-scale analysis

# Chapter 2

# Demersal cephalopod communities in the Mediterranean – a large-scale analysis

## 2.1 Abstract

Cephalopod assemblages at the scale of the entire Mediterranean Sea were analysed using information from two decades of standardized scientific bottom trawl surveys. Western and eastern communities were compared using a combined approach of multivariate ordination techniques and non-linear regressions. This methodology enabled us to distinguish community assemblages and simultaneously analyse the influence of geographic, bathymetric and environmental (sea surface temperature and Chlorophyll *a* concentration) gradients on observed community patterns. While little differences in species composition were found between sub-basins, the relative contribution of species differed. Bathymetry was shown to be a common structural driver for the cephalopod communities of both basins, and three communities were distinguished (shallow water, upper slope and middle slope). Winter temperature showed comparatively higher influence in the western basin while winter productivity showed the smallest, but consistent influence on community assemblages in both basins. Thus, the environmental parameters analysed did not cause an immediate change in cephalopod assemblages, but affected the communities with a time lag of several months. Observed differences in the importance of environmental drivers show that different processes operate in the two basins. Obtained results contribute to establish similarities and differences between Mediterranean basins regarding the important ecosystem functional group of cephalopods. The gained information should be useful to comply with the principles of integrative and ecosystemic management approaches nowadays aimed for in fisheries and conservation management.

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## 2.2 Introduction

The Mediterranean Sea is characterized by strong regional differences. The influence of river inflows, Atlantic waters and the Suez canal, amongst others, cause differences in sedimentation and hydrography (Millot, 2005; Rossi et al., 2014) as well as environmental gradients in temperature, salinity and productivity (D'Ortenzio and Ribera d'Alcalà, 2009). Anthropogenic influences also vary among regions (Coll et al., 2012), and the influence of Lessepsian migrants declines from east to west (Golani, 1998). Given these contrasting local conditions and the reduced water exchange between basins through the Strait of Sicily, the western and the eastern Mediterranean basins are considered rather different ecosystems (Piroddi et al., 2015a). Marine species have different tolerances and habitat preferences and therefore these contrasting conditions are expected to produce differences in faunal communities.

Community analyses at the scale of the whole Mediterranean have only focused on fish so far, most of them with a focus on species diversity and marine protected areas

(Gaertner et al., 2007; Granger et al., 2015; Mouillot et al., 2011). Only one recent work exists on the diversity of cephalopods (Keller et al., 2016 / Chapter 3), a species group of key importance for ecosystem functioning (André et al., 2010; Hunsicker et al., 2010). In spite of the socio-economic importance of cephalopods in Mediterranean countries, no study has been conducted on their assemblages on a large scale, comparing different Mediterranean communities in areas of contrasting environmental conditions. This is remarkable, as at species level, cephalopods are species very sensitive to environmental influences, a fact that has been highlighted in various studies already (Lloret et al., 2001; Pierce et al., 2008; Keller et al., 2014; Puerta et al., 2014).

This taxon has gained in importance in many areas worldwide, due to various reasons. On one hand, increasing abundances have been reported for many years, probably due to ecosystem changes (Balguerías, 2000; Doubleday et al., 2016; Vecchione et al., 2009; Keller et al, accepted / Chapter 4). On the other hand, due to the depletion of many commercial fish stocks, cephalopods became an increasingly important fishery resource (FAO Sofia 2016). Therefore, many studies have focused on Mediterranean cephalopod communities (e.g. Relini and Orsi-Relini, 1984; Quetglas et al., 2014, 2000; see Krstulovic Sifner et al., 2005 for a summary of works in the eastern basin), but only at local scale. As the structure of a community depends on bathymetric, hydrographic and biological features (e.g. depth, temperature, salinity, productivity), contrasting external regimes are likely to influence cephalopods at the community level. While depth has often been found to structure local cephalopod communities (Sanchez et al., 1998; Quetglas et al., 2000; Krstulovic Sifner et al., 2005), other physical factors like temperature and Chlorophyll a content are rarely included (González and Sánchez, 2002). Given the fact that they are commonly reported as important drivers of diversity distribution patterns (Moutin and Raimbault, 2002; Rosa et al., 2008a, 2008b; Siddon et al., 2011), their influence on community structure may be assumed and has been already proven for different marine communities (Siddon et al., 2011; Hidalgo et al., 2014).

The present work analyses cephalopod communities at the whole Mediterranean scale using fishery-independent data from annual standardized scientific trawl surveys. Our objective is to determine differences in cephalopod communities at Mediterranean scale and identify possible drivers of these differences. To this end, we compare cephalopod communities in the western and eastern Mediterranean basins applying a combination of community analyses and non-linear regression techniques. Our specific objectives were a) to differentiate species assemblages, b) to identify the most characteristic species of each assemblage, and c) to investigate possible drivers of assemblage structure. The results may serve as a baseline for ongoing changes of marine ecosystems at the whole Mediterranean scale, as overfishing and climate change will certainly affect species distribution ranges and therefore community composition in the future.

## 2.3 Material and methods

### 2.3.1 Biological sampling

Biological data were obtained from the international Mediterranean bottom trawl surveys MEDITS (http://www.sibm.it/MEDITS%202011/principalemedits.htm), which are conducted every year between May and August from 1994 until today, covering depths from 10 m down to 800 m. The surveys are performed annually by all riparian EU countries, in addition to Montenegro and Albania, and currently are the most valuable data source to investigate demersal ecosystems in the Mediterranean Sea. The sampling methodology is standardized among all the countries (for details see Bertrand et al., 2002; A.A.V.V., 2016). The MEDITS area is divided into geographical sub-areas (GSA's; Fig 1) established by the General Fisheries Commission for the Mediterranean (GFCM, http://www.fao.org/gfcm/en/).

A stratified random sampling design is used for this survey, with bathymetric strata comprising 10-50, 51-100, 101-200, 201-500 and 501-800 m. The standardized gear used is a GOC-73 trawl with a cod-end mesh size of 20 mm and a vertical and horizontal opening of the net of about 2 m and 18 m respectively (Bertrand et al., 2002). The net opening is measured by an attached underwater gear opening monitor system, which allows calculating the swept area. Trawling is conducted at daylight, with a towing speed of 3 knots and hauls duration of 30 and 60 minutes over shelf and slope grounds respectively. Abundance data for each species are standardized to number of individuals per $km^2$ using the swept area method (Saville, 1977; Souplet, 1996).

For the compilation of the species list, all data from 1994 -2012 were used, while the community analysis was based on data from 2003 – 2008. Data from the selected years represent the best compromise between continuous sampling, wide geographical range, reasonable temporal scale and available satellite data. Some areas sampled only in recent years were excluded from the analysis and data for 2007 for the Greek waters are missing, as no survey was conducted there that year. The final dataset for this analysis included 6258 sampling stations with cephalopod records.

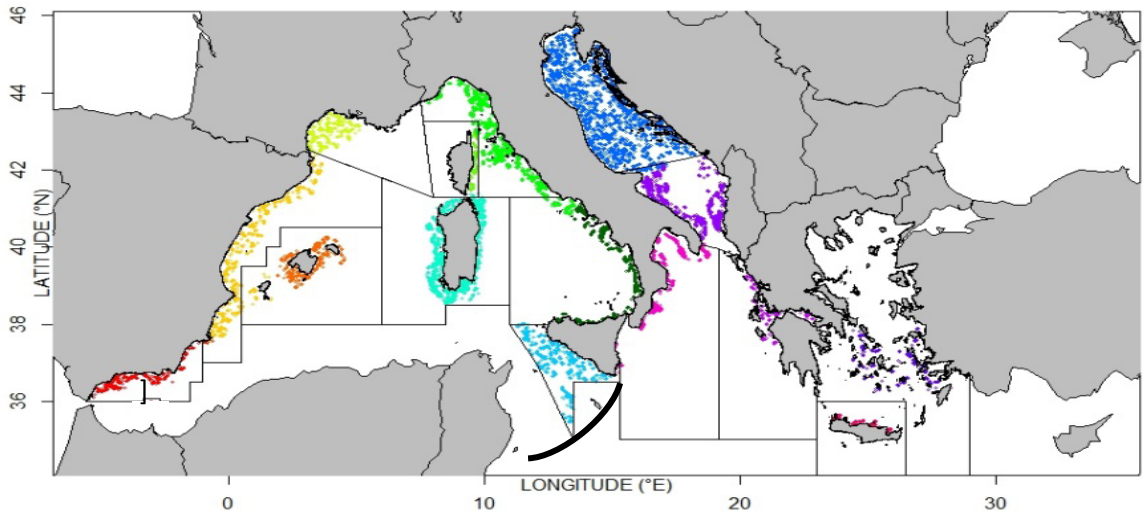



Figure 2.1: Map of the Mediterranean Sea showing the MEDITS sampling stations included in the analysis (2003-2008). The thick black line shows the division into western and eastern basin used in this study, while thin black lines represent the geographical subareas (GSAs) established by the GFCM and used as spatial units in the survey.

### 2.3.2 Satellite data

Satellite data for SST and Chla resulted from MODIS-Aqua and NPP-VIIRS sensors measurements already processed with regional ocean colour algorithms (resolution 1 km, daily data) and were downloaded from the MyOcean database (http://marine.copernicus.eu/web/69-interactive-catalogue.php). Both temperature and Chla concentration (proxy for food availability) might influence ecological and metabolic processes differently at different stages of the animal's life history, and Chla is expected to show a time-lagged response due to the time required for energy transfer between trophic levels. Both parameters were therefore modelled using different seasonal means: 1) the spring (March-May) concurrent with the survey and 2) the preceding winter (December-February). These months were chosen as they proofed to be good descriptors of the key oceanographic processes determining spring productivity in the Mediterranean (Lloret et al., 2001; Quetglas et al., 2011; Puerta et al., 2016b). Means were calculated for each of the geographical sub-divisions within the MEDITS program (GSAs), and each sampling station was assigned to its respective GSA in the modelling. This approach was the best compromise between the higher environmental variability of single stations and the regional spatial scale of the modelled response (regional community composition).

### 2.3.3 Community analysis

Due to contrasting oceanographic conditions between the western and eastern Mediterranean sub-basins, the data analysis was conducted separately for both basins (Fig 2.1). To describe gradients in species composition relative to environmental drivers, we used a combination of community analyses (nonmetric multidimensional scaling, NMDS) and non-linear regressions (general additive modelling, GAM). This combined methodology has already been used in marine communities before and is useful to reveal spatial and / or temporal differences in community structure as functions of relevant covariates (Siddon et al., 2011; Muenchow et al., 2013; Hidalgo et al., 2014). First, NMDS was applied to the community dataset to reduce the community composition information of each station to 3 major modes of variability (NMDS axes). NMDS is an ordination technique which arranges samples (in our case stations) in the best way to match the observed similarities between communities. NMDS separates communities along multiple dimensions, with the first axis accounting for the major part of the variance. Data were $4^{th}$ root transformed to reduce the importance of species occurring in very high densities. Transformation was followed by data standardization to species maxima to allow better comparison between species occurring at very different abundance levels (Field et al., 1982). Then, Bray-Curtis similarity matrices among all different stations were computed and analysed by NMDS ordination using 50 runs to find the best model solution (R-library "vegan"). The resulting 3 ordination axes of the NMDS plot gave three dimensionless scores (one for each axis) per station, which were then used as response variables in the non-linear GAMs (R-library "mgcv").

Covariates used to explain differences in cephalopod assemblages were sampling location, depth, SST and Chla, as these parameters represent important geographic, bathymetric and environmental gradients. One-dimensional smoothers were used to describe the bathymetric and environmental influence, while a two-dimensional smoother

was used combining latitude and longitude to represent a potential geographic gradient remaining in the data once environmental and bathymetric influence was taken into account. The degree of freedom of the smoothers was restricted to k=3 for depth and to k=4 for the environmental variables. The general model structure for each axis was as follows:

$$\text{Axis NMDS } 1,2,3 \sim s(\text{Lat, Long}) + s(\text{depth}) + s(\text{Chla}_{\text{Winter}}) + s(\text{SST}_{\text{Summer}}) + s(\text{Chla}_{\text{Spring}}) + s(\text{SST}_{\text{Spring}})$$

While SST was normally distributed, Chla values were log-transformed to obtain normalized distributions. A step-wise procedure was adopted for model selection, removing one non-significant covariate ($p<0.05$) at a time from the full model. In addition, covariates displaying non-significant effect (i.e. 95% intervals containing zero value in the partial effects plots) in most of the range of variation of the covariate were not included in the best model. Best model selection was then based on the minimization of both the Generalized Cross-Validation (GCV) and the Akaike Information Criterion (AIC). For all GAMs, residual plots were checked and confirmed the assumptions of variance homogeneity and normal distribution. Finally, to identify the species most correlated to the respective axis and therefore most characteristic for the observed community composition, Spearman rank correlations were used with the obtained significances posteriori corrected by Bonferroni.

## 2.4 Results

In total, 40 and 41 species or species complexes (e.g. *Alloteuthis* spp.) representing 17 different families were included in the analysis of the western and eastern basin respectively. During the MEDITS surveys of 1994-2012, species only caught in the western basin are *Stoloteuthis leucoptera, Ommastrephes bartramii* (only in the Strait of Sicily), *Ocythoe tuberculata* and *Opisthoteuthis calypso* (only in the Iberian Sea) (Table 2.1). *Ancistrocheirus lesueurii, Pyroteuthis margaritifera* and *Abraliopsis morisii* were only recorded in the eastern basin (Ionian Sea), as well as *Octopoteuthis sicula*, a species only found in the Ionian and Aegean Sea. *Chtenopteryx sicula* and *Chiroteuthis veranii* have been found in both basins, but only in Italian waters (Tyrrhenian and Ionian Sea). *Bathypolypus sponsalis* has not been caught in the easternmost parts of the Mediterranean (Adriatic and the Aegean Sea).

While species with the highest frequencies of occurrence were the same in both basins, their relative contribution changed between basins: *Eledone cirrhosa* (59%), *Alloteuthis* spp. (54%) and *Illex coindetii* (46%) predominated in the western basin, but *Illex coindetii* (62%), *Alloteuthis* spp. (62%) and *Eledone cirrhosa* (33%) in the eastern.

Once the community data of each basin was analysed by NMDS, GAMs were applied to model the three most important axes. The three best models for each axis and basin are shown in table 2.2.

Table 2.1: List of all species found during the MEDITS surveys, by basin. Numbers are frequency of occurence averaged from 1994-2012. Species only sampled in the western / eastern basin are marked in grey / rose respectively.

| Species | WESTERN BASIN | EASTERN BASIN |
|---|---|---|
| **Order SEPIIDA** | | |
| **Family Sepiidae** | | |
| *Sepia elegans* Blainville, 1827 | 25.48 | 31.88 |
| *Sepia officinalis* Linneus, 1758 | 6.98 | 8.38 |
| *Sepia orbignyana* Férussac, 1826 | 24.76 | 16.98 |
| *Sepia* spp. | 0.64 | 0.25 |
| **Family Sepiolidae** | | |
| *Sepiola affinis* Naef, 1912 | 0.11 | 0.33 |
| *Sepiola intermedia* Naef, 1912 | 0.78 | 1.8 |
| *Sepiola ligulata* Naef, 1912 | 0.23 | 0.82 |
| *Sepiola robusta* Naef, 1912 | 0.22 | 2.2 |
| *Sepiola rondeleti* Leach, 1817 | 0.45 | 0.34 |
| *Sepiola* spp. | 12.58 | 14.23 |
| *Rondeletiola minor* Naef, 1912 | 9.75 | 10.47 |
| *Sepietta obscura* Naef, 1916 | 0.33 | 0.39 |
| *Sepietta neglecta* Naef, 1916 | 0.27 | 0.88 |
| *Sepietta oweniana* (D'Orbigny in Férussac & d'Orbigny) | 24.97 | 11.79 |
| *Sepietta* spp. | 2.22 | 5.47 |
| **Unid. Sepiolinae** | 0.52 | 1.13 |
| *Rossia macrosoma* (Delle Chiaje, 1830) | 12.68 | 7.36 |
| *Neorossia caroli* (Joubin, 1902) | 5.81 | 2.52 |
| *Heteroteuthis dispar* (Ruppell, 1844) | 2.31 | 1.52 |
| *Stoloteuthis leucoptera* (Verrill, 1878) | 0.34 | 0 |
| **ORDER MYOPSIDA** | | |
| **Family Loliginidae** | | |
| *Alloteuthis media* (Linnaeus, 1758) | 34.16 | 55.05 |
| *Alloteuthis subulata* Lamarck, 1798 | 12.89 | 6.16 |
| *Alloteuthis* spp. | 7.2 | 1.72 |
| *Loligo forbesii* Steenstrup, 1856 | 10.23 | 3.36 |
| *Loligo vulgaris* Lamarck, 1798 | 15.51 | 31.34 |
| *Loligo* spp. | 0.91 | 0.09 |
| **ORDER OEGOPSIDA** | | |
| **Family Ommastrephidae** | | |
| *Ommastrephes bartramii* (LeSueur, 1821) | 0.01 | 0 |
| *Illex coindetii* (Verany, 1839) | 46.49 | 62.59 |
| *Todarodes sagittatus* (Lamarck 1798) | 18.41 | 7.19 |
| *Todaropsis eblanae* (Ball, 1841) | 28.4 | 21.1 |
| **Family Histioteuthidae** | | |
| *Histioteuthis bonnellii* (Férussac, 1835) | 5.46 | 2.52 |
| *Histioteuthis reversa* (Verrill, 1880) | 5.25 | 4.86 |
| *Histioteuthis* spp. | 0.15 | 0.03 |
| **Family Onychoteuthidae** | | |
| *Ancistroteuthis lichtensteinii* Orbigny, 1839 | 1.92 | 1.01 |
| *Onychoteuthis banksii* (Leach, 1817) | 0.27 | 0.23 |

| Species | WESTERN BASIN | EASTERN BASIN |
|---|---|---|
| **Family Enoploteuthidae** | | |
| *Abralia veranyi* (Rüppell, 1844) | 10.88 | 7.06 |
| *Abraliopsis morisii* (Vérany, 1839) | 0 | 0.02 |
| Unid. Enoploteuthidae | 0 | 0.05 |
| **Family Chtenopterygidae** | | |
| *Chtenopteryx sicula* (Veranyi, 1851) | 0.02 | 0.02 |
| **Family Octopoteuthidae** | | |
| *Octopoteuthis sicula* Rüppell, 1844 | 0 | 0.11 |
| Family Chiroteuthidae | | |
| *Chiroteuthis veranii* (Férussac, 1835) | 0.01 | 0.15 |
| **Family Ancistrocheiridae** | | |
| *Ancistrocheirus lesueurii* (Orbigny, 1842) | 0 | 0.06 |
| **Family Brachioteuthidae** | | |
| *Brachioteuthis riisei* (Steenstrup, 1882) | 0.27 | 0.12 |
| Family Pyroteuthidae | | |
| *Pyroteuthis margaritifera* (Rüppell, 1844) | 0 | 0.05 |
| **ORDER OCTOPODA** | | |
| **Family Octopodidae** | | |
| *Octopus vulgaris* Cuvier, 1798 | 25.48 | 12.21 |
| *Callistoctopus macropus* Risso, 1826 | 0.35 | 0.4 |
| *Octopus salutii* (Verany, 1839) | 11.46 | 5.98 |
| *Macrotritopus defilippi* (Vérany, 1851) | 1.3 | 0.29 |
| *Octopus* spp. | 0.12 | 0.09 |
| *Pteroctopus tetracirrhus* (Delle Chiaje, 1830) | 12.02 | 2 |
| *Scaeurgus unicirrhus* (Orbigny, 1840) | 18.51 | 8.94 |
| *Bathypolypus sponsalis* (P. & H. Fischer, 1892) | 5.37 | 0.03 |
| *Eledone cirrhosa* (Lamarck, 1798) | 59.26 | 33.67 |
| *Eledone moschata* (Lamarck, 1798) | 16.91 | 28.93 |
| **Family Ocythoidae** | | |
| *Ocythoe tuberculata* Rafinesque, 1814 | 0.01 | 0 |
| **Family Argonautidae** | | |
| *Argonauta argo* Linnaeus, 1758 | 0.03 | 0.03 |
| **Family Opisthoteuthidae** | | |
| *Opisthoteuthis calypso* Villanueva et al., 2002 | 0.03 | 0 |
| *Opisthoteuthis* spp. | 0.01 | 0 |

Table 2.2: Best model selection based on explained deviance (%DEV) and Akaike Information Criterion. The three best GAMs for each axis and basin are shown (best models in grey). Significant covariates ($p<0.05$) entering in the models are marked by +. Chla Spring / Chla Winter: Mean chlorophyll *a* concentration during spring / winter. SST Spring / SST Winter: Mean SST during spring / winter.

WESTERN BASIN

| | Location | Depth | SST Winter | SST Spring | Chla Winter | Chla Spring | %DEV | AIC |
|---|---|---|---|---|---|---|---|---|
| AXIS 1 | + | + | + | | | | 76.2 | 3809.8 |
| | + | + | | | | | 76.1 | 3824.6 |
| | | + | | | | | 74.1 | 4079.9 |
| AXIS2 | + | + | + | | | | 25.6 | 2304.9 |
| | + | + | | | | | 25.1 | 2326.9 |
| | | + | | | | | 15.1 | 2754.5 |
| AXIS 3 | + | + | | | + | | 12.8 | 2654.9 |
| | + | + | | | | | 12.3 | 2672.3 |
| | + | | | | | | 10.8 | 2731.7 |

EASTERN BASIN

| | Location | Depth | SST Winter | SST Spring | Chla Winter | Chla Spring | %DEV | AIC |
|---|---|---|---|---|---|---|---|---|
| AXIS 1 | + | + | | | | | 68.1 | 3848.9 |
| | | + | | | | | 62.4 | 4190.0 |
| | + | | | | | | 44.0 | 5198.9 |
| AXIS2 | + | + | | | | | 45.4 | 951.0 |
| | + | | | | | | 41.7 | 1102.0 |
| | | + | | | | | 3.20 | 2263.6 |
| AXIS 3 | + | + | + | + | + | | 20.5 | 1431.8 |
| | + | + | | + | + | | 19.1 | 1461.3 |
| | + | + | | | + | | 18.6 | 1473.7 |

In the western basin, the first axis of the NMDS mainly describes the depth gradient of the cephalopod community, as seen by the linear depth effect in our GAM model (Fig 2.2 a). Deep-sea assemblages are positively related to the axis values and consist of species like *Todarodes sagittatus, Histioteuthis bonnellii, H. reversa* and *Bathypolypus sponsalis* (Table 2.3). More coastal communities show a negative correlation and are characterized mainly by demersal species like *Octopus vulgaris, Alloteuthis* spp., *Eledone moschata* and *Loligo vulgaris* (Table 2.3). In addition to depth, winter SST influenced the community composition and was included in the best model with low temperature values related to positive axis 1 scores. The remaining spatially structured variance captured by the geographic pattern reveals that north-westernmost waters (i.e. Gulf of Lions and Catalan coast) and south-westernmost waters off the Italian mainland and Sicily were related with more positive values of axis 1.

Axis 2 mainly distinguishes upper slope communities as evidenced by the dome-shaped form of the bathymetric effect (Fig 2.2 b). The species positively related with this axis were *Todaropsis eblanae*, *Sepietta oweniana, Octopus salutii, Abralia veranyi, Rossia macrosoma* and *Scaeurgus unicirrhus* (Table 2.3). Winter SST also was a significant driver affecting the spatial variability of this axis (Fig 2.2 b). Upper slope communities are favoured by warmer waters at the surface, as positive values of axis 2 are positively correlated to higher temperature values. *Todarodes sagittatus* and *Alloteuthis* species, on the other hand benefit from colder waters (Table 2.3). The remaining variance captured by the spatial effect reveals a gradient from the west to the east of the basin, with positively correlated species favoured in the eastern areas.

Species positively related to Axis 3 were primarily influenced by greater depth, while those negatively linked with the axis were related to relatively high values of winter concentration of Chla (Fig 2.2 c). Those species associated to more productive areas consisted mainly of *Sepia orbignyana, Illex coindetii, Scaeurgus unicirrhus, Todaropsis eblanae* and *Sepia elegans* (Table 2.3). The spatial effect reveals the most favourable conditions for these communities (i.e. negative correlation with the axis 3) in the strait of Sicily (Fig 2.2 c).

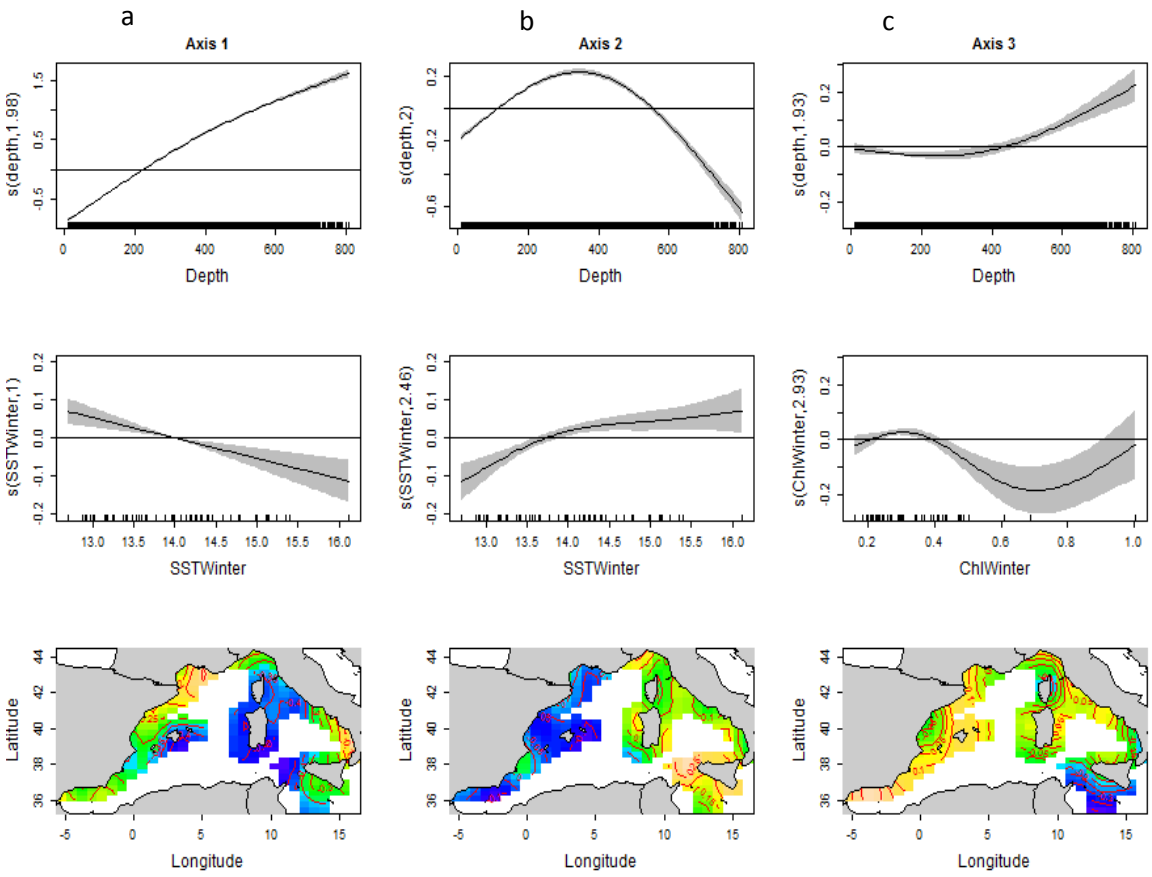



Figure 2.2: Results of the GAM analysis performed on (a) axis 1, (b) axis 2 and (c) axis 3 of the NMDS results for the western basin. Plotted are the significant partial effects of each model (fitted line) together with 95% confidence intervals (dashed lines). The maps show the geographical effects of the sampling locations. The colour gradient of the geographical effect codes from low values (darker colours) to high values (lighter colours).

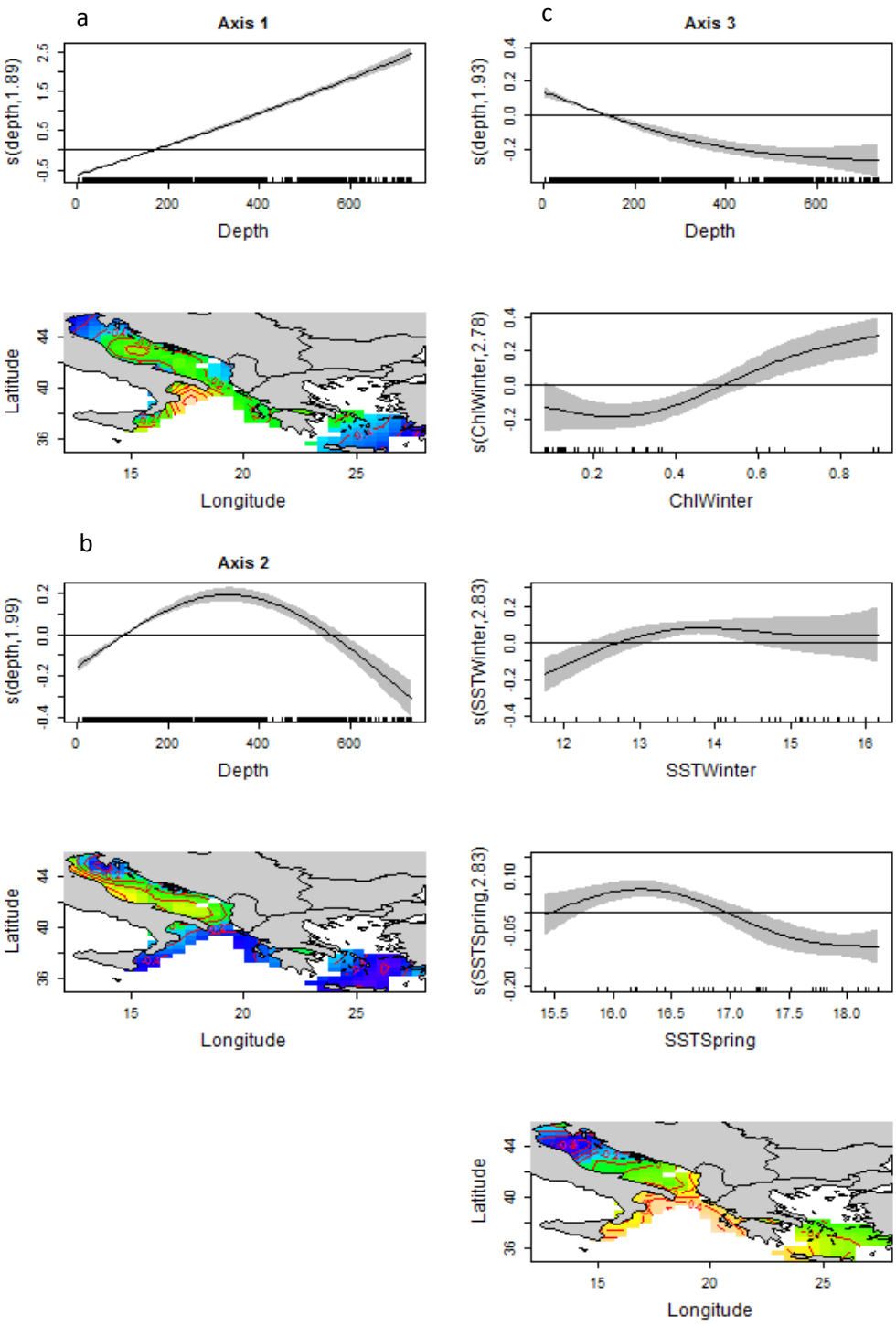



Figure 2.3: Results of the GAM analysis performed on (a) axis 1, (b) axis 2 and (c) axis 3 of the NMDS results for the eastern basin. Plotted are the significant partial effects of each model (fitted line) together with 95% confidence intervals (dashed lines). Note that y-axes are at the scales of the response variables for each axis. The maps show the geographical effects of the sampling locations. The colour gradient of the geographical effect codes from low values (darker colours) to high values (lighter colours).

Table 2.3: Spearman rank correlations of the 3 axes (dimensions) from the non-metric multidimensional scaling (NMDS) correlated with taxa density. Only significant correlations ≥0.20 (for positive correlations, in green) and ≤(-0.2) (for negative correlations, in rose) are shown. Numbers (n) and means of the significant correlations are shown for each group.

| WESTERN BASIN | | | | | |
|---|---|---|---|---|---|
| **Axis 1** | | **Axis 2** | | **Axis 3** | |
| n=6; mean= -0.50 | | n=2; mean= -0.253 | | n=6; mean= -0.218 | |
| *Octopus vulgaris* | -0.63 | *Todarodes sagitattus* | -0.30 | *Sepia orbignyana* | -0.53 |
| *Alloteuthis* spp. | -0.60 | *Alloteuthis* spp. | -0.21 | *Illex coindetii* | -0.39 |
| *Eledone moschata* | -0.52 | | | *Scaeurgus unicirrhus* | -0.32 |
| *Loligo vulgaris* | -0.49 | | | *Todaropsis eblanae* | -0.24 |
| *Sepia elegans* | -0.38 | | | *Sepia elegans* | -0.23 |
| *Sepia officinalis* | -0.38 | | | *Alloteuthis* spp. | -0.22 |
| n=10; mean= 0.31 | | n=9; mean= 0.308 | | n=3; mean= 0.264 | |
| *Todarodes sagitattus* | 0.53 | *Todaropsis eblanae* | 0.57 | *Octopus vulgaris* | 0.35 |
| *Histioteuthis bonnellii* | 0.37 | *Sepietta oweniana* | 0.44 | *Sepia officinalis* | 0.24 |
| *Bathypolypus sponsalis* | 0.32 | *Octopus salutii* | 0.30 | *Eledone moschata* | 0.20 |
| *Histioteuthis reversa* | 0.31 | *Abralia veranyi* | 0.28 | | |
| *Abralia veranyi* | 0.31 | *Rossia macrosoma* | 0.25 | | |
| *Octopus salutii* | 0.27 | *Scaeurgus unicirrhus* | 0.24 | | |
| *Neorossia caroli* | 0.27 | *Rondeletiola minor* | 0.24 | | |
| *Todaropsis eblanae* | 0.27 | *Pteroctopus tetracirrhus* | 0.23 | | |
| *Rossia macrosoma* | 0.26 | *Loligo forbesii* | 0.21 | | |
| *Pteroctopus tetracirrhus* | 0.21 | | | | |
| EASTERN BASIN | | | | | |
| **Axis 1** | | **Axis 2** | | **Axis 3** | |
| n=5; mean= -0.421 | | n=6; mean= -0.347 | | n= 1; mean= -0.237 | |
| *Eledone moschata* | -0.59 | *Sepia elegans* | -0.55 | *Illex coindetii* | -0.24 |
| *Loligo vulgaris* | -0.54 | *Eledone moschata* | -0.50 | | |
| *Alloteuthis* spp. | -0.41 | *Octopus vulgaris* | -0.27 | | |
| *Sepia officinalis* | -0.36 | *Scaeurgus unicirrhus* | -0.27 | | |
| *Sepia elegans* | -0.20 | *Sepia orbignyana* | -0.26 | | |
| | | *Loligo forbesii* | -0.23 | | |
| n=12; mean= 0.299 | | n=3; mean= 0.327 | | n=6; mean= 0.308 | |
| *Todarodes sagitattus* | 0.45 | Eledone cirrhosa | 0.54 | *Loligo vulgaris* | 0.44 |
| *Todaropsis eblanae* | 0.44 | *Todaropsis eblanae* | 0.24 | *Octopus vulgaris* | 0.39 |
| *Eledone cirrhosa* | 0.35 | *Illex coindetii* | 0.20 | *Todaropsis eblanae* | 0.34 |
| *Illex coindetii* | 0.31 | | | *Sepia officinalis* | 0.27 |
| *Abralia veranyi* | 0.31 | | | *Sepietta oweniana* | 0.21 |
| *Rossia macrosoma* | 0.30 | | | *Eledone moschata* | 0.20 |
| *Histioteuthis reversa* | 0.30 | | | | |
| *Scaeurgus unicirrhus* | 0.25 | | | | |
| *Rondeletiola minor* | 0.24 | | | | |
| *Octopus salutii* | 0.23 | | | | |
| *Neorossia caroli* | 0.21 | | | | |
| *Sepia orbignyana* | 0.20 | | | | |

Regarding the eastern basin we find very congruent results with the western in terms of the bathymetry delineating the communities associated with each axis. The first axis describes a bathymetric gradient of the communities (Fig 2.3 a). The composition of the shallow water community is similar to the western basin but differs in the most characteristic species: *Eledone moschata* in the eastern basin and *Octopus vulgaris* in the west (Table 2.3). The slope community consists of various species, being the most important ones *Todarodes sagitattus*, *Todaropsis eblanae*, *Eledone cirrhosa* and *Illex coindetii*. A regional effect is evident around the Gulf of Taranto, a region more positively associated to the communities than the rest of the eastern basin.

The second axis describes the upper slope communities, as already seen in the western basin (Fig 2.3 b). Communities are characterised by species with an intermediate depth spectrum like *Eledone cirrhosa, Todaropsis eblanae* and *Illex coindetii* (Table 2.3). Regional effects are positively influencing this assemblage on the west coast of the northern Adriatic Sea.

The third axis is not influenced only by depth or geographic position, but also by environmental parameters like the productivity regime during winter (Chla Winter) as well as by the temperatures during winter and spring (Fig 2.3 c). Species positively correlated with the axes (*Loligo vulgaris, Octopus vulgaris, Todaropsis eblanae, Sepia officinalis* and others) are favoured by higher productivity during winter, intermediate to high winter temperatures (SST) and low SST in spring (Fig 2.3 c, Table 2.3). Regional effects fostering these communities occur in the Ionian Sea, while the northern Adriatic is a favourable habitat for *Illex coindetii*, the only important species negatively correlated with the third axis (Table 2.3).

## 2.5 Discussion

Despite the contrasting oceanographic conditions governing the western and the eastern Mediterranean basins, the communities show very little difference in species composition, while they do differ in the relative species contribution. Bathymetry was shown to be a common structural driver for the cephalopod communities of both basins. Clearly, three communities were distinguished: the continental shelf communities, upper slope and middle slope communities, consistent with previous studies at local scale (Sanchez et al., 1998; Quetglas et al., 2000; González and Sánchez, 2002). Sea surface temperature, particularly in winter, shows comparatively higher influence in the western basin (affecting the communities depicted by the axes 1 and 2) while in the eastern it only had a significant influence on axis 3. Productivity resulted to have a similar, although weak influence on community assemblages in both basins (exclusively associated with the third axis). In all axes and the two basins, the models detected geographic differentiation in the communities once the bathymetric and the environmental gradients were taken into account, suggesting that additional regional scale drivers not included in our models affect cephalopods communities.

Community composition

Although the Strait of Sicily is a geographical hindrance for deep-sea cephalopod species, the faunistic lists in both basins are very similar, and differ mostly in the abundances of single species. While the higher temperature and the lower productivity of the eastern basin might favour certain species, they do not impede the occurrence of most species. As already pointed out, basins vary in their characteristics, which in turn may influence the mechanisms at community level. The fact that the presence of the same species leads to varying species contribution within the two sub-basins may hint to different ecological processes, as for example trophic pathways. Indeed, food web structures are different from region to region, with the eastern basin containing a lower proportion of small pelagic fish and other organisms of low trophic levels (Tsagarakis et al., 2010; Halouani et al., 2015). The relative total biomass of small pelagic fish per $km^2$ is higher in the western basin and the Adriatic Sea than in the eastern regions (Piroddi et al., 2015a). In addition, due to different exploitation patterns and food web structures the impact of fishing varies from basin to basin (Halouani et al., 2015). According to Hattab et al. (2013), the different Mediterranean ecosystems also differ in flows of biomass and community energetic attributes, leading to structural differences in different regions.

Our study reveals that *Eledone moschata* is the most characteristic shelf species in the eastern basin, followed by *Loligo vulgaris*, while in the west, it is *Octopus vulgaris* followed by *Alloteuthis* species. In general, *O. vulgaris* is of little importance in shallow waters in the eastern basin, which coincides with its lower abundances in that basin (Belcari et al., 2002a). Reasons for this could potentially be stronger fishing pressure on juvenile octopus in that area (valuable fishery resource), but also species-specific preferences. For example, findings of Sobrino et al. (2002), Vargas-Yáñez et al. (2009) and Keller et al. (accepted / Chapter 4) support the hypothesis that higher SST negatively affects *Octopus vulgaris* abundance, while Puerta et al. (2016) found that *Octopus* landings were positively related with Chla concentration. Hence the high temperatures and the low productivity of the eastern basin could be reasons of its lower importance. Another possibility is that this species inhabits shallower waters in the eastern zones, as already observed for other cephalopod species (Tursi and D'Onghia, 1992; Quetglas et al., 2000). If this is the case, their underrepresentation in the eastern basin could be due to the legal sampling restrictions in waters shallower than 50 m. In general, *Eledone* species and *Illex coindetii* are more characteristic in eastern communities than in the western basin, while *Alloteuthis* species are more predominant in the west. This may be a result of species-specific preferences. For example, *Illex coindetii* seems to be favoured by higher temperatures and more oligotrophic areas (Lauria et al., 2016; Puerta et al., 2015, Keller et al., accepted / Chapter 4), which is consistent with our results.

Comparing the species lists of both basins, few differences were obvious. Most of the species only found in some areas are very rarely sampled during MEDITS surveys, so conclusions about their real presence in certain areas should be drawn with care. For example, *Ommastrephes bartramii* and *Ocythoe tuberculata* did not appear in our eastern basin samples but have been recorded various times from the Aegean Sea and both Aegean and Levantine Sea respectively (Salman, 2009).

Drivers of cephalopod community patterns

In both basins, cephalopod communities are divided into different sub-communities by depth. This was certainly expected, since depth has already been evidenced as the main factor structuring cephalopod communities of different regions at a smaller scale (Quetglas et al., 2000; González and Sánchez, 2002; Krstulovic Sifner et al., 2005). Results of these studies are mostly in congruence with the present work, with the same or similar indicator species for the distinct communities (Quetglas et al., 2000; González and Sánchez, 2002; Soriano et al., 2003). It is worth noticing, however, that although the communities are shaped by depth with an identical functional relationship (Figs 2.2 and 2.3), the most relevant species and the relative contribution of species for the very same communities differ in each basin.

Apart from depth, environmental conditions have been demonstrated to influence community composition. In almost all models, significant variables are based on winter values, indicating that environmental effects do not act immediately, but time-lagged. It is various months before the survey that the communities are most susceptible to external influences, suggesting that environmental conditions are of special importance during the paralarval and early life stages of cephalopods. At that life stage, conditions will affect survival and abundance of different species differently, fostering a common spring-summer community of specific structure. Such a time-lagged effect has already been seen in cephalopods both in the Mediterranean (Lloret et al., 2001; Vargas-Yáñez et al., 2009; Quetglas et al., 2011; Puerta et al., 2015) and the Atlantic Ocean (Sobrino et al., 2002; Pierce et al., 2005).

In line with this, winter sea surface temperature ($SST_{Winter}$) is an important structuring factor. It influences community composition more in the western than in the eastern basin, as in the latter it only affects communities delineated by the third axis, while in the west, its influence is visible in the first and second axes. This observation is in accordance with recent research (Keller et al., in review / Chapter 4, Puerta et al. 2015), which shows that, at a species level (e.g. *O. vulgaris* and *I. coindetii*), species in the western basin are grouped at smaller scale according to spatial differences in environmental variability such as regional gradients of winter temperature. By contrast, in the eastern basin, species displayed synchronic variability in the whole sub-basin, with absence of population sub-structuring (Keller et al., in review / Chapter 4).

While deep-sea communities benefit from lower temperatures, higher SST during winter favoured shallow water and upper slope communities. As most cephalopods spend relatively little time at the surface, SST will probably influence early life stages rather than adults, especially for deeper water species (Pierce et al., 2008). In contrast, young animals often spend much time in coastal waters (e.g. Sepiidae, Loliginidae) or belong to the plankton (e.g. Ommastrephidae). Therefore temperature was included using a time lag of several months, and indeed winter temperature resulted more important than spring temperature. Milder winter temperatures likely enhanced the survival of young life stages and result in higher growth rates and competitiveness with fishes. The presence of ommastrephid paralarvae, for example, has been shown to be positively influenced by temperature (Zaragoza et al., 2014). So far, little is known about the importance of temperature on cephalopods at community level (but see González and Sánchez, 2002),

but studies at species level have shown that different species show different preferences and physiological optima (see e. g. Robin and Denis 1999; Lauria et al., 2016; Sobrino et al., 2002; Vargas-Yáñez et al., 2009). Colder winter temperatures, on the other hand, cause stronger and deeper mixing of Mediterranean water masses through cascading events and convection via stronger winds or more frequent thunderstorms. Enhanced mixing leads to higher nutrient availability, with positive effects up the food chain. In the eastern basin, both spring and winter temperatures are of importance. This could result from the fact that the distribution of *I. coindetii*, the species which characterizes the community linked to negative axis values, is partly driven by spring temperatures (Keller et al., in review / Chapter 4).

The productivity showed the smallest, but consistent influence in our study, as it was captured by the third axis of both the eastern and western NMDS. Shallow water communities benefit from higher Chlorophyll *a* content (Chla). This may be due to a more direct influence of primary productivity on the food webs in shallower waters. In coastal food-webs, filtration feeders and other secondary producers rapidly convert biomass and make it accessible for organisms higher in the food web. Reaction time of shallow water communities may therefore be quicker, making the communities more sensible to changes in food availability. On the other hand, low winter productivity shows a much smaller effect, which can be linked to *I. coindetii* species (Table 2.3). This is in accordance with former findings, which show a negative effect of higher productivity on the abundance of this squid at different spatial scales (Puerta et al., 2015, Keller et al., accepted / Chapter 4). There it was hypothesised that this is due to the fact that small pelagic fishes are effective competitors for food with early and juvenile stages of squid. As their survival and growth is usually fostered by higher Chla contents, areas of lower productivity may be advantageous for juvenile squid.

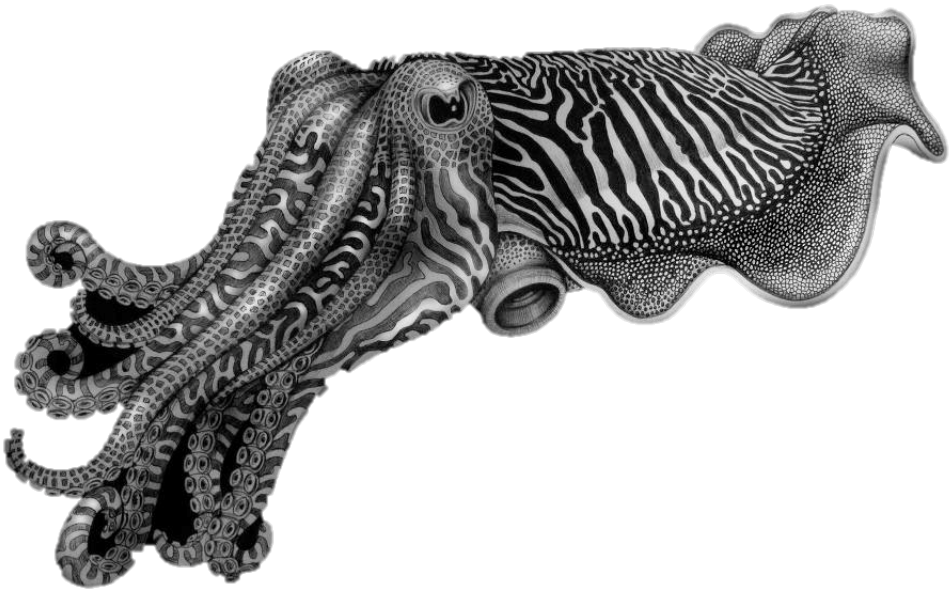
Regional effects play a role in both basins, suggesting the influences of additional drivers on the community composition that are spatially structured but not included in our models. These effects are different for each of the communities differentiated by the three axes of the NMDS, meaning that drivers affect different communities in different ways. The bottom type, for example, will have important implications on the relative distribution of demersal species. Various other effects are at play and probably entangled, e.g. an influence on cephalopod distributions may result from river inflows (lower salinity, more nutrients, higher turbidity, higher pollution), Atlantic water inflow (less saline and colder water, larval supply), local wind regimes (increased mixing of water masses) or fishing pressure (selective pressure on certain species or their predators and food). River inflow has been proved to influence the abundances of certain cephalopod species including *O. vulgaris* and *I. coindetii* (Lloret et al., 2001; Puerta et al., 2014, 2016). The gradient seen for the second axis in the western basin (Fig 2.2 b) could hint to an influence of Atlantic water masses or current pattern, which transport different water masses to the different sub-basins. These Atlantic water masses not only differ in their characteristics, but may also transport cephalopod paralarvae into - and within - the Mediterranean (Bouchet and Taviani, 1992).

Conclusions and further research

The present study is the first one on cephalopod assemblages at the scale of the entire Mediterranean Sea. Assemblages in the two basins basically differ in relative importance of species within the communities, but very little regarding general species composition. At this large scale, depth has been confirmed as the most important factor structuring cephalopod communities, but additional influences of environmental variability have been revealed and hold different ranks in both basins.

We expect that these results will contribute to infer and understand the responses of cephalopod communities to changing environmental conditions especially in the framework of the current global change and overexploitation of most Mediterranean stocks (Colloca et al., 2013; Vasilakopoulos et al., 2014). Given the observed sensibility of communities to temperature, we may expect that the ongoing climate warming will cause changes in community compositions. According to our models, this change would be more evident in the western basin, where the influence of temperature is stronger.

The understanding of the processes influencing community composition may be beneficial for fisheries and conservation management, areas that nowadays utilize the Integrated Ecosystem Approach (IEA) and therefore require knowledge at community level. In this context, a useful extension of our work would be to integrate other factors like salinity and bottom type, which play important roles in the distribution of demersal species (Demestre et al., 2000; González and Sánchez, 2002).



# Chapter 3

# Large-scale spatio-temporal patterns of Mediterranean cephalopod diversity

# Chapter 3

# Large-scale spatio-temporal patterns of Mediterranean cephalopod diversity

## 3.1 Abstract

Species diversity is widely recognized as an important trait of ecosystems' functioning and resilience. Understanding the causes of diversity patterns and their interaction with the environmental conditions is essential in order to effectively assess and preserve existing diversity. While diversity patterns of most recurrent groups such as fish are commonly studied, other important taxa such as cephalopods have received less attention. In this work we present spatio-temporal trends of cephalopod diversity across the entire Mediterranean Sea during the last 19 years, analysing data from the annual bottom trawl survey MEDITS conducted by 5 different Mediterranean countries using standardized gears and sampling protocols. The influence of local and regional environmental variability in different Mediterranean regions is analysed applying generalized additive models, using species richness and the Shannon Wiener index as diversity descriptors. While the western basin showed a high diversity, our analyses do not support a steady eastward decrease of diversity as proposed in some previous studies. Instead, high Shannon diversity was also found in the Adriatic and Aegean Seas, and high species richness in the eastern Ionian Sea. Overall diversity did not show any consistent trend over the last two decades. Except in the Adriatic Sea, diversity showed a hump-shaped trend with depth in all regions, being highest between 200-400 m depth. Our results indicate that high Chlorophyll *a* concentrations and warmer temperatures seem to enhance species diversity, and the influence of these parameters is stronger for richness than for Shannon diversity.

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## 3.2 Introduction

Species diversity has strong implications on the functioning and conservation state of ecosystems. Its preservation should therefore be a priority in conservation management, and indeed many protected areas are established based on the diversity hotspots they sustain. Understanding the causes of underlying diversity patterns and their interaction with the environmental conditions are of paramount importance for its conservation. Species distributions are not always explicable by their physiological constraints, and the mechanisms structuring diversity patterns are often unknown (Ben Rais Lasram et al., 2009). On a global scale, different drivers have been proposed up to now, including factors like ecosystem productivity, climate and habitat heterogeneity, as well as historical causes or geographical barriers (Rahbek and Graves, 2001). The latitudinal gradient (poleward decrease) of diversity is the most striking pattern and has been investigated for different marine taxa (e.g. Macpherson and Duarte, 1994, Rex et al., 1993, Macpherson, 2002). In the marine environment, sea temperature and productivity

are commonly reported as the main drivers of geographical distribution patterns of diversity (Moutin and Raimbault, 2002; Rosa et al., 2008a, 2008b; Siddon et al., 2011).

The Mediterranean Sea is a semi-enclosed basin characterized by pronounced longitudinal gradients in temperature and productivity. Accordingly, an eastward decreasing trend in fish species richness has been reported by some authors (Quignard and Tomasini, 2000; Ben Rais Lasram et al., 2009; Coll et al., 2010). This trend has often been explained by the large-scale eastward decline in primary production which is observed in the Mediterranean (Moutin and Raimbault, 2002), arguing that areas of high food availability serve as feeding and reproduction sites for many species (Coll et al., 2010). Temperature regime is another possible determinant of diversity, affecting the competitiveness of animals via their different temperature tolerances and mobility (Siddon et al., 2011). In addition to food supply and temperature, the inflow of Atlantic water and human influences have been identified as local-scale factors structuring patterns of spatial diversity in the Mediterranean (Bianchi and Morri, 2000; Gaertner et al., 2007; Coll et al., 2012).

While there have been some studies on Mediterranean fish diversity (Gaertner et al., 2007, 2013; Granger et al., 2015), no large scale analysis of Mediterranean cephalopod diversity exists. This contrasts with the fact that they play a key role in marine ecosystems, as they are important prey species as well as voracious predators (André et al., 2010). Therefore, fluctuations in their community composition and abundance are likely to have profound consequences for the food webs and ecosystems. Furthermore, cephalopods are important living resources for most Mediterranean countries, sustaining some economically important fisheries in various areas (FAO, 2012). Being semelparous species with a short generation time of normally one to two years, they can respond rapidly to changes in environmental conditions (Pierce et al., 2008). Temporal changes in their abundance and diversity can therefore supply important information about ecosystem alterations. Despite their importance, the only existing publications looking at their large-scale diversity patterns are species inventories comparing species richness between the Adriatic Sea, the western and the eastern Mediterranean basin (Mangold, K. & Boletzky, 1988; Bello, 2004). Mangold and Boletzky (Mangold, K. & Boletzky, 1988) conclude a general eastward decrease in species numbers and found the Adriatic to contain the lowest species richness, but the more recent study of Bello (Bello, 2004) noted fewer differences between the areas. This is characteristic for species inventories, which, although historically very precious, suffer from biases resulting from different sampling intensities (Hortal et al., 2008). More analytical cephalopod diversity studies are restricted to local scales, both in the western (Quetglas et al., 2000, 2014; González and Sánchez, 2002) and the eastern (Lefkaditou et al., 2003; Krstulovic Sifner et al., 2005; Salman, 2009) basins. At such local scales, depth was found to be the main diversity driver.

Understanding and monitoring species diversity is a crucial issue in confined areas with substantial human influences such as the Mediterranean Sea (Bianchi and Morri, 2000). Climate change (Coma et al., 2009), resource exploitation (Colloca et al., 2013; Vasilakopoulos et al., 2014), pollution (Danovaro, 2003) and other anthropogenic influences like habitat loss and the introduction of alien species (Coll et al., 2012) steadily impact the local diversity, with unknown implications for the concerned area. Despite this, few diversity studies covering the whole longitudinal gradient of the Mediterranean Sea

exist until now, and long-time data series based on standardized protocols are rare (but see (Gaertner et al., 2007, 2013; Granger et al., 2015)). One dataset of this kind results from the international Mediterranean bottom trawl survey MEDITS, which is performed every spring since 1994 (Bertrand et al., 2002). Due to its regular realization, large-scale coverage, the length of the time series and the standardization of methodology, this dataset is one of the most valuable data sources to investigate large scale patterns of demersal species abundance and diversity in the Mediterranean Sea.

Using the MEDITS dataset we investigate the relationship between demersal cephalopod diversity and environmental characteristics. The aim of this work is two-fold. First, we explore cephalopod spatio-temporal diversity patterns in the Mediterranean, using the entire time series of MEDITS cruises currently available (19 years). Secondly, using a shorter time series, we analyse the influence of putative environmental covariates on the spatial and temporal variation of cephalopod diversity.

## 3.3 Material and methods

### 3.3.1 Data sources

The international Mediterranean bottom trawl survey MEDITS (http://www.sibm.it/MEDITS%202011/principalemedits.htm) is performed by all riparian EU countries, and also by Montenegro and Albania. The sampling was performed under repeated international standardized protocol (for details see Bertrand et al., 2002). Most of the authors participate consistently in the surveys of the MEDITS programme. Since 1994, the survey is conducted every year in spring / early summer (May-August) and covers depths from 10 m down to 800 m. The MEDITS area is divided into different geographical sub-areas (GSA's; Fig 3.1), established by the General Fisheries Commission for the Mediterranean (http://www.fao.org/gfcm/en/). The sampling procedure is standardised, with a common sampling protocol and strategy in place and the same gear employed throughout the whole study zone (Bertrand et al., 2002). The area of available data ranges from 5.21° W to 27.75° E, and from 35.22° to 45.65° N across the national waters of 10 countries (Fig 3.1). A stratified random sampling design is used for this survey, with bathymetric strata comprising 10-50, 51-100, 101-200, 201-500 and 501-800 m. The standardized gear used is a GOC 73 trawl with a cod-end mesh size of 20 mm and a vertical and horizontal opening of the net of about 2 m and 18 m, respectively (Bertrand et al., 2002). The net opening is measured by an attached underwater Scanmar system, which allows calculating the swept area. Trawling is conducted at daylight, with a towing speed of 2-3 knots and hauls duration of 30 and 60 minutes over shelf and slope grounds respectively. Haul catches are sorted to species level whenever possible. Abundance data for each species are standardized to number of individuals per $km^2$ using the swept area method.

### 3.3.2 Diversity measures and modelling approach

Two different diversity measures, widely used in fishery studies, were selected for this study in order to capture the main axes of biodiversity variability: the Shannon-

Wiener Diversity (H') and the species richness index (S). While S is the total number of species, H' takes into account the number of species as well as their contribution within a sample (evenness). Given the same number of species, samples with more even abundances (i.e., less dominant species) have a higher H'. Garofalo et al. (Garofalo et al., 2007) evaluated correlations among different indices of diversity performing Spearman rank tests and showed that the Shannon Wiener index evidenced the strongest positive correlation with the other indices they analyzed. In this study, S and H' were chosen as they give complementary information. Other diversity indices (e.g. Simpsons index or rarity) have not been used to avoid redundancy (Gaertner et al., 2013). Both indices were calculated based on species abundance data.

Prior to final analyses, exploratory analyses of spatio-temporal trends were performed on all data from 1994-2012. Some areas only sampled in recent or in very few years where excluded from these analyses (GSA 2, GSA 15, GSA 25). Greece (GSA 20, 22, 23) did not conduct the MEDITS surveys in 2002, 2007 and in 2009-2012, so the overall Mediterranean diversity in recent years is not completely comparable to former years. Also, in some years and areas around Greece, not all cephalopod species were recorded; therefore the respective surveys were excluded as well. In 1997, GSA 23 had to be excluded for this reason, and therefore few stations were sampled in the Southern Aegean Sea in that year. In the same area, all samples between 1998-2001 had to be excluded. Despite these deficiencies, the Greek data were included as they represent the easternmost data points of the time series. The final dataset included 15 GSAs and comprised 18214 hauls (Fig 3.1).

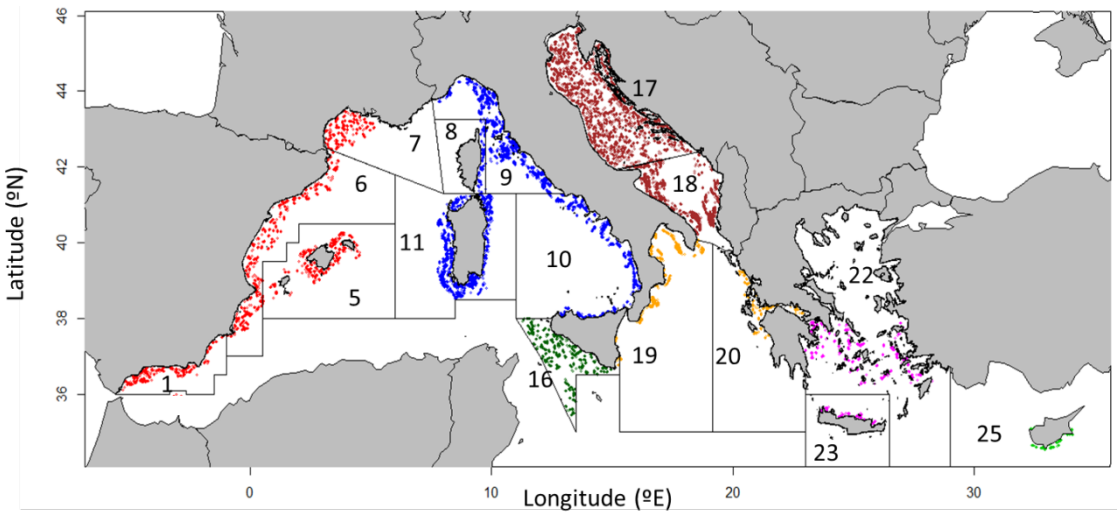



Figure 3.1: Map of the Mediterranean Sea showing the geographical sub-areas (GSAs) established by the General Fisheries Commission for the Mediterranean (GFCM) and the MEDITS stations sampled stations during 1994-2013 (20238 hauls).

For analysis purpose, the Mediterranean was divided into 6 biogeographical zones modified from Gaertner el al. (2013) (Fig 3.2). These bioregions represent ecologically meaningful units rather than artificial management units as do the GSAs. As diversity index values are scale-dependent, different spatial scales (haul, GSA and bioregion) are

considered. We computed the diversity at haul scale (α-diversity) and the total diversity over all hauls both per GSA (γ-diversity) and per bioregion. As species richness per spatial unit depends on the sampling effort, the number of total species at each bioregion / GSA was rarefied to 35 / 20 hauls respectively (Granger et al., 2015). Sample-based rarefaction is a method to calculate species richness for a given number of individual samples by randomly re-sampling the pool of N samples many times; then the average number of species found in each sample can be calculated (Gotelli NJ and Colwell RK, 2011). In our case, the use of 35 /20 hauls was a trade-off between excluding areas with less hauls and having a representative sample size for all regions (trials were also made with different numbers of hauls but gave the same pattern). Furthermore, species accumulation curves, which show the accumulated number of species for each additional sample taken, were calculated; these curves reach an asymptote once further sampling does not yield any new species.

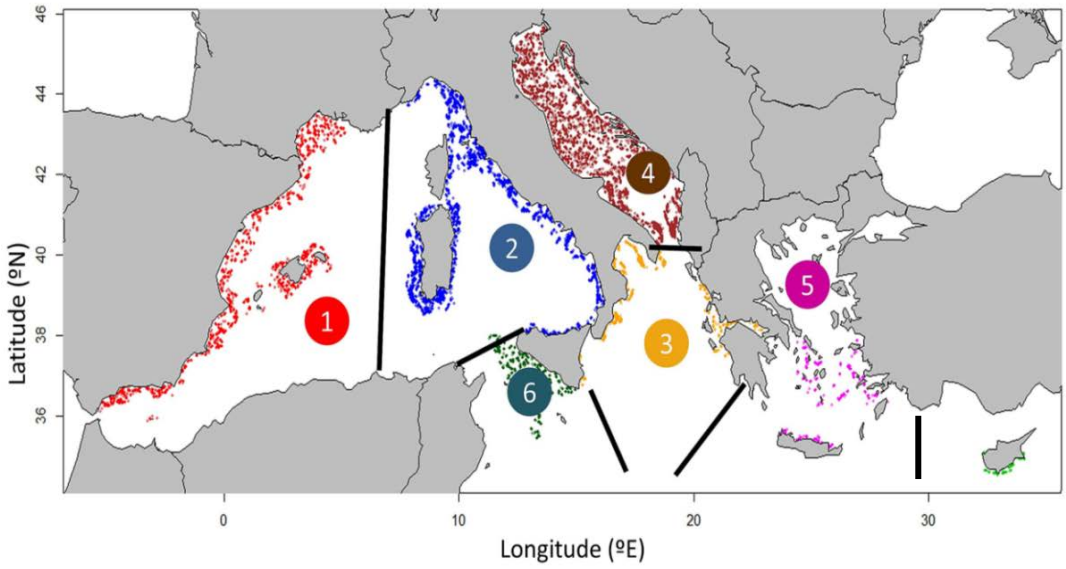



Figure 3.2: Map of the Mediterranean Sea showing the MEDITS stations sampled during 1994-2012. Plotted are 20463 hauls and colours correspond to the following bioregions: 1) Iberian-Lions, 2) Tyrrhenian Sea, 3) Adriatic Sea, 4) Ionian Sea, 5) Aegean Sea and 6) Strait of Sicily. Separation of bioregions is marked with thick black lines.

To analyse synchrony of trends between bioregions, Pearson correlation coefficients were calculated between the time series of the six bioregions. Correlation coefficients, diversity indices, rarefaction and species accumulation curves were calculated in R (version 2.15.1; http://www.r-project.org/) using the vegan package (2.0-10).

When modeling putative drivers of H' and S, only surveys from 2003-2008 were included, as in these years most areas were sampled consistently. To account for the skewed sampling in shallower areas where very few hauls deeper than 700 m were available, only hauls down to this depth were considered. The final data used came from 15 GSAs and comprised 6275 hauls. As we do not have prior expectations on the relationships between diversity and its drivers and cannot exclude the occurrence of non-

linearity, Generalized Additive Models (GAMs) were used. A two-dimensional smoother was used combining latitude and longitude to account for the spatial effect. The variable 'year' was considered as factor, while for 'depth', a general effect was tested versus various regional effects (where depth was modelled separately for each bioregion) as we expected spatial differences. Mean seasonal chlorophyll *a* concentration (Chla; $mg \cdot m^{-3}$) and Sea Surface Temperature (SST; ºC) were averaged across GSAs; whereas SST was normally distributed, Chla values were log-transformed to obtain normalized distributions. Chla concentration was used as a proxy for food availability and was modelled using seasonal means of the winter (December-February) and spring (March-May) preceding the survey, in order to account for the time required for energy transfer between trophic levels. The same two seasons were used to calculate mean seasonal SST, as temperature might influence ecological and metabolic processes differently at different stages of the animal's life history. These covariates and periods of year have been selected as good descriptors of the main oceanographic processes determining spring productivity in the Mediterranean (Lloret et al., 2001; Quetglas et al., 2011). Chla and SST data were obtained from satellite-derived products available on the Giovanni NASA webpage (http://gdata1.sci.gsfc.nasa.gov). The model formulation was as follows:

Species diversity: $H' \sim$ Year + s(Lat, Long) + Depth*Bioregion + s(Chla) + s(SST)
Species richness: $S \sim$ Year + s(Lat, Long) + Depth*Bioregion + s(Chla) + s(SST)

Best model selection was based on the minimization of both the Generalized Cross-Validation (GCV) and the Akaike Information Criterion (AIC). All GAM analyses were carried out with R using the mgcv library (1.7-29). For all GAMS, residual plots were checked and confirmed the assumptions of variance homogeneity and normal distribution. Using decorrelation plots, we assured the existence of spatial autocorrelation of the diversity index values, a prerequisite to build spatial models. Finally, residuals were checked for the absence of spatial correlation with directional variograms and spatial plotting of residuals, assuring us that the model covariates account for the spatial variation of diversity.

## 3.4 Results

During all cruises, a total of 58 species or taxa of cephalopods were found (see Table 3.1), of which 47 were determined to species level. In spite of the large number of sampling stations analysed, the species accumulation curves (Fig 3.3) have not completely leveled off in most bioregions, which means that additional sampling is required to catch all the regional cephalopod diversity.

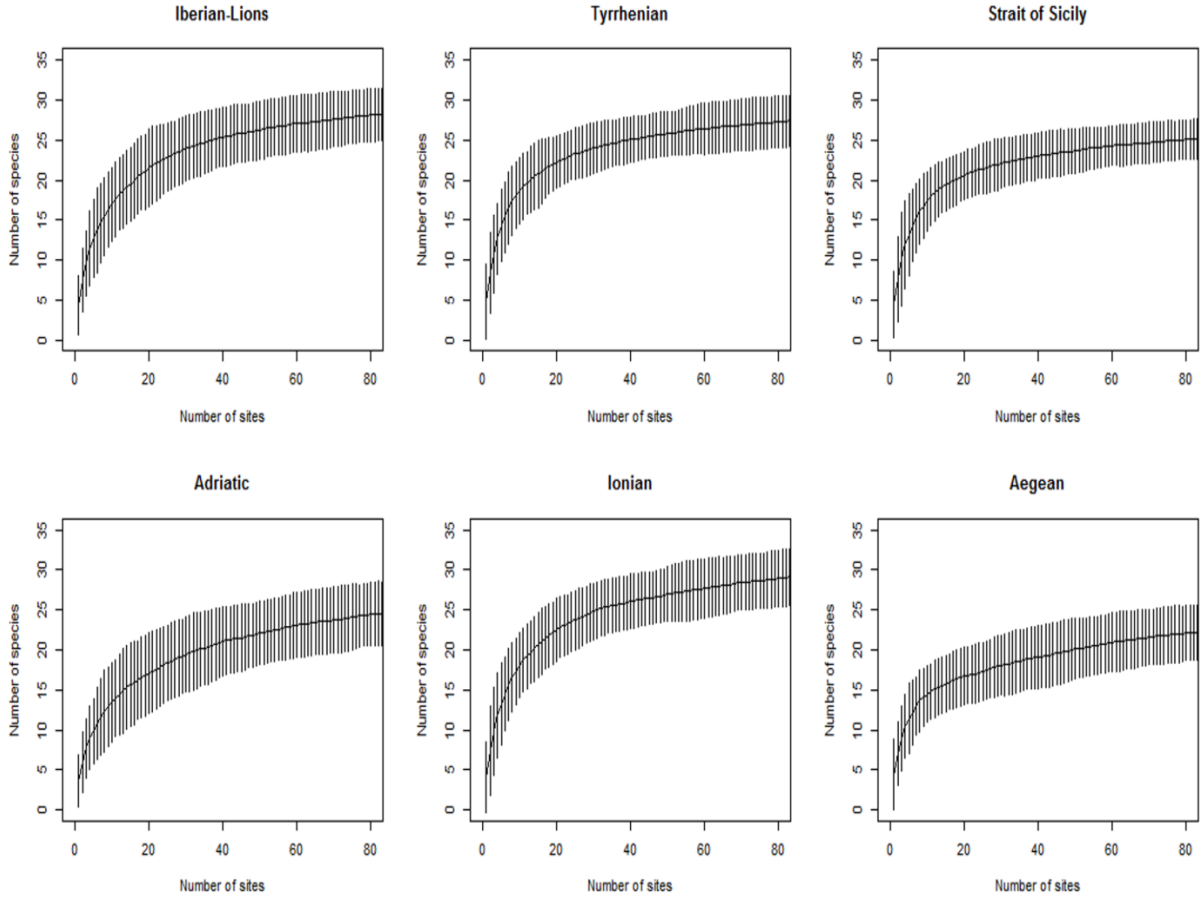



Figure 3.3: Species accumulation curves of MEDITS sampling at different Mediterranean bioregions.

Table 3.1: List of all species found during MEDITS, by area. Numbers are frequency of occurence averaged from 1994-2012. Species marked in grey were excluded from the modeling. *Alloteuthis media*, *Alloteuthis subulata* and *Alloteuthis* sp. were joined for the analysis.

| Species | Iberian-Lions | Tyrrhenian | Ionian | Adriatic | Aegean | Strait of Sicily |
|---|---|---|---|---|---|---|
| **Order SEPIIDA** | | | | | | |
| **Family Sepiidae** | | | | | | |
| *Sepia elegans* Blainville, 1827 | 28.84 | 23.13 | 29.76 | 31.93 | 38.94 | 26.42 |
| *Sepia officinalis* Linneus, 1758 | 6.79 | 6.54 | 3.76 | 9.17 | 15.83 | 9.5 |
| *Sepia orbignyana* Férussac, 1826 | 20.69 | 28.4 | 14.08 | 14.58 | 55.28 | 20.01 |
| *Sepia spp.* | 0.23 | 0.56 | 0 | 0.35 | 0 | 2.16 |
| **Family Sepiolidae** | | | | | | |
| *Sepiola affinis* Naef, 1912 | 0.15 | 0.05 | 0.14 | 0.41 | 0 | 0.29 |
| *Sepiola intermedia* Naef, 1912 | 0.75 | 0.43 | 4.04 | 1.23 | 0.25 | 2.45 |
| *Sepiola ligulata* Naef, 1912 | 0.08 | 0.38 | 1.39 | 0.71 | 0 | 0 |
| *Sepiola robusta* Naef, 1912 | 0.4 | 0.14 | 0.91 | 2.79 | 0 | 0 |
| *Sepiola rondeleti* Leach, 1817 | 0.03 | 0.74 | 0.77 | 0.24 | 0 | 0.36 |
| *Sepiola spp.* | 17.05 | 9.35 | 2.37 | 18.67 | 5.53 | 14.33 |
| *Rondeletiola minor* Naef, 1912 | 8.02 | 11.89 | 19.09 | 8.5 | 2.26 | 5.04 |
| *Sepietta obscura* Naef, 1916 | 0.05 | 0.58 | 0 | 0.54 | 0 | 0 |
| *Sepietta neglecta* Naef, 1916 | 0.2 | 0.37 | 0.07 | 1.21 | 0 | 0 |
| *Sepietta oweniana* (D'Orbigny in Férussac & d'Orbigny) | 20.87 | 29.16 | 21.46 | 9.54 | 3.02 | 17.85 |
| *Sepietta spp.* | 0.05 | 4.03 | 0.14 | 7.59 | 0 | 0.29 |
| **Unid. Sepiolinae** | 0 | 0 | 0 | 0 | 18.34 | 4.39 |
| *Rossia macrosoma* (Delle Chiaje, 1830) | 10.56 | 14.29 | 11.08 | 5.32 | 17.59 | 11.52 |
| *Neorossia caroli* (Joubin, 1902) | 3.87 | 7.4 | 5.09 | 1.77 | 2.01 | 4.18 |
| *Heteroteuthis dispar* (Ruppell, 1844) | 2.34 | 2.7 | 5.51 | 0.28 | 1.51 | 0.5 |
| *Stoloteuthis leucoptera* (Verrill, 1878) | 0.63 | 0.24 | 0 | 0 | 0 | 0 |
| | | | | | | |
| **ORDER MYOPSIDA** | | | | | | |
| **Family Loliginidae** | | | | | | |
| *Alloteuthis media* (Linnaeus, 1758)[1] | 52.25 | 21.99 | 30.1 | 66.32 | 14.07 | 37.15 |
| *Alloteuthis subulata* Lamarck, 1798[1] | 27.58 | 3.87 | 2.44 | 7.83 | 0.25 | 11.45 |
| *Alloteuthis spp.*[1] | 3.6 | 10.61 | 0 | 0.02 | 27.64 | 2.16 |
| *Loligo forbesii* Steenstrup, 1856 | 3.65 | 15.51 | 5.02 | 0.67 | 28.64 | 5.33 |
| *Loligo vulgaris* Lamarck, 1798 | 13.08 | 16.58 | 15.05 | 36.97 | 24.62 | 17.64 |
| *Loligo spp.* | 1.63 | 0.66 | 0 | 0 | 1.51 | 0 |
| **ORDER OEGOPSIDA** | | | | | | |
| **Family Ommastrephidae** | | | | | | |
| *Ommastrephes bartramii* (LeSueur, 1821) | 0 | 0 | 0 | 0 | 0 | 0.07 |
| *Illex coindetii* (Verany, 1839) | 45.54 | 45.78 | 53.8 | 64.48 | 72.36 | 52.41 |
| *Todarodes sagittatus* (Lamarck 1798) | 21.75 | 14.16 | 12.2 | 4.82 | 16.58 | 28.01 |
| *Todaropsis eblanae* (Ball, 1841) | 12.7 | 35.12 | 27.87 | 20.35 | 5.28 | 43.12 |
| **Family Histioteuthidae** | | | | | | |
| *Histioteuthis bonnellii* (Férussac, 1835) | 3.22 | 6.49 | 6.83 | 1.38 | 0.25 | 7.27 |
| *Histioteuthis reversa* (Verrill, 1880) | 4.4 | 6.36 | 14.36 | 2.25 | 1.01 | 2.66 |
| *Histioteuthis spp.*[3] | 0.1 | 0 | 0.07 | 0.02 | 0 | 0.94 |
| **Family Onychoteuthidae** | | | | | | |
| *Ancistroteuthis lichtensteinii* Orbigny, 1839 | 4.32 | 0.8 | 3.97 | 0.11 | 0.75 | 0.07 |
| *Onychoteuthis banksii* (Leach, 1817) | 0.5 | 0.11 | 0.63 | 0.09 | 0.5 | 0.29 |
| **Family Enoploteuthidae** | | | | | | |
| *Abralia veranyi* (Rüppell, 1844) | 9.18 | 10.76 | 21.53 | 3.07 | 1.26 | 16.27 |
| *Abraliopsis morisii* (Vérany, 1839) | 0 | 0 | 0.07 | 0 | 0 | 0 |
| Unid. Enoploteuthidae | 0 | 0 | 0 | 0 | 0.75 | 0 |

| Species | Iberian-Lions | Tyrrhenian | Ionian | Adriatic | Aegean | Strait of Sicily |
|---|---|---|---|---|---|---|
| **Family Chtenopterygidae** | | | | | | |
| *Chtenopteryx sicula* (Veranyi, 1851) | 0 | 0.03 | 0.07 | 0 | 0 | 0 |
| **Family Octopoteuthidae** | | | | | | |
| *Octopoteuthis sicula* Rüppell, 1844 | 0 | 0 | 0.42 | 0 | 0.25 | 0 |
| **Family Chiroteuthidae** | | | | | | |
| *Chiroteuthis veranii* (Férussac, 1835) | 0 | 0.02 | 0.7 | 0 | 0 | 0 |
| **Family Ancistrocheiridae** | | | | | | |
| *Ancistrocheirus lesueurii* (Orbigny, 1842) | 0 | 0 | 0.28 | 0 | 0 | 0 |
| **Family Brachioteuthidae** | | | | | | |
| *Brachioteuthis riisei* (Steenstrup, 1882) | 0.78 | 0 | 0.35 | 0 | 0.75 | 0 |
| **Family Pyroteuthidae** | | | | | | |
| *Pyroteuthis margaritifera* (Rüppell, 1844) | 0 | 0 | 0.21 | 0 | 0 | 0 |
| | | | | | | |
| **ORDER OCTOPODA** | | | | | | |
| **Family Octopodidae** | | | | | | |
| *Octopus vulgaris* Cuvier, 1798 | 34.6 | 21.63 | 16.52 | 9.39 | 29.4 | 16.7 |
| *Callistoctopus macropus* Risso, 1826 | 0.25 | 0.42 | 0.28 | 0.48 | 0 | 0.36 |
| *Octopus salutii* (Verany, 1839) | 10.91 | 12.5 | 7.25 | 6.06 | 0.5 | 8.35 |
| *Macrotritopus defilippi* (Vérany, 1851) | 2.29 | 0.88 | 0.07 | 0.39 | 0 | 0.36 |
| *Octopus spp.* | 0.08 | 0.16 | 0 | 0.13 | 0 | 0.07 |
| *Pteroctopus tetracirrhus* (Delle Chiaje, 1830) | 6.21 | 16.08 | 4.74 | 1.08 | 2.76 | 10.37 |
| *Scaeurgus unicirrhus* (Orbigny, 1840) | 7.87 | 23.61 | 21.39 | 3.4 | 28.39 | 25.99 |
| *Bathypolypus sponsalis* (P. & H. Fischer, 1892) | 9.38 | 3.87 | 0.14 | 0 | 0 | 0.65 |
| *Eledone cirrhosa* (Lamarck, 1798) | 62.91 | 63.41 | 27.32 | 36.97 | 18.34 | 30.09 |
| *Eledone moschata* (Lamarck, 1798) | 18.83 | 13.91 | 11.92 | 33.85 | 33.17 | 24.91 |
| **Family Ocythoidae** | | | | | | |
| *Ocythoe tuberculata* Rafinesque, 1814 | 0.03 | 0 | 0 | 0 | 0 | 0 |
| **Family Argonautidae** | | | | | | |
| *Argonauta argo* Linnaeus, 1758 | 0 | 0 | 0.14 | 0 | 0 | 0.29 |
| **Family Opisthoteuthidae** | | | | | | |
| *Opisthoteuthis calypso* Villanueva et al., 2002 | 0.08 | 0 | 0 | 0 | 0 | 0 |
| *Opisthoteuthis spp.* | 0.03 | 0 | 0 | 0 | 0 | 0 |

### 3.4.1 Exploratory analysis

The 47 cephalopods determined at species level were included in this analysis. When joining all data from 1994-2012 and rarefying species number to 35 hauls, the highest and lowest median species richness recorded were 24 and 16 species in the Ionian and Aegean Sea respectively (Fig 3.4). While the Iberian-Lions (S=23.88) region and the Tyrrhenian Sea (S=23.93) also showed high species richness, the Adriatic Sea (S=19.10) and the Strait of Sicily (S=19.75) yielded comparatively fewer species.

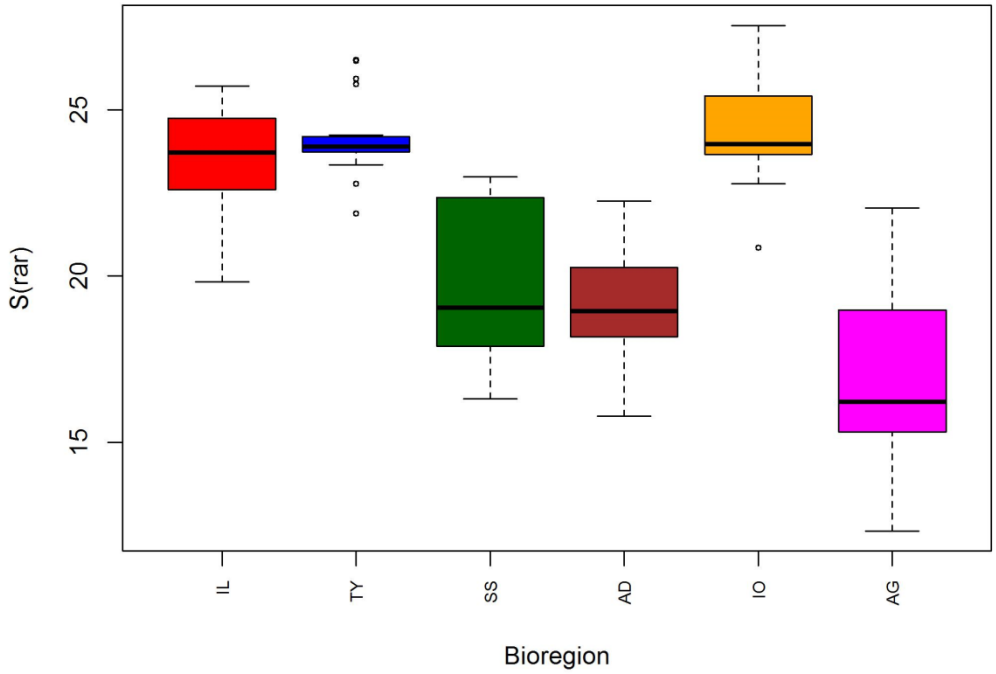



Figure 3.4: Boxplot of total species richness ($S_{rar}$) at different Mediterranean bioregions: Iberian-Lions (IL), Tyrrhenian Sea (TY), Strait of Sicily (SS), Adriatic Sea (AD), Ionian Sea (IO) and Aegean Sea (AG). Samples were included from 1994-2012 and rarefied to 35 hauls.

Except in the Aegean Sea, Shannon diversity (H') and species richness (S) per haul (α-diversity) showed the same bioregional trend, being highest in the Tyrrhenian Sea and lowest in the Adriatic Sea (Fig 3.5). In the Aegean Sea, H' and S showed contrasting values, with S being very high but H' comparatively low. Species richness within one GSA (Gamma diversity) shows a quite variable pattern, from a median of 14 species (GSA 7) to 22 species (GSA 1 and 9) (Fig 3.6). The Alboran Sea, the Catalan Sea and the Balearic Sea are characterized by a high number of cephalopod species, and similar high richness values can be found in the Tyrrhenian (GSA 9, 10) and the Ionian Sea (GSA 19, 20). The waters around the Strait of Sicily (GSA 16) and Sardinia (GSA 11) are slightly less diverse, and the lowest richness can be found in the Gulf of Lions (GSA 7), the Sea around Corsica (GSA 8) and the Adriatic and Southern Aegean Sea.

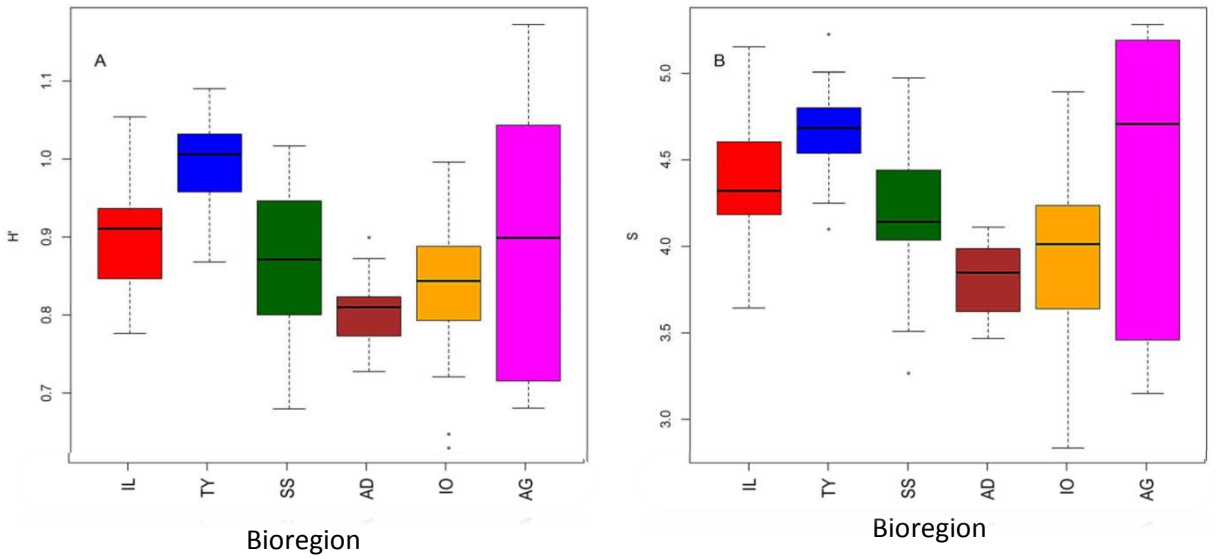



Figure 3.5: Shannon diversity (A) and Species richness (B) per haul from MEDITS sampling (1994-2012), calculated for the following bioregions: Iberian-Lions (IL), Tyrrhenian Sea (TY), Strait of Sicily (SS), Adriatic Sea (AD), Ionian Sea (IO) and Southern Aegean Sea (AG).

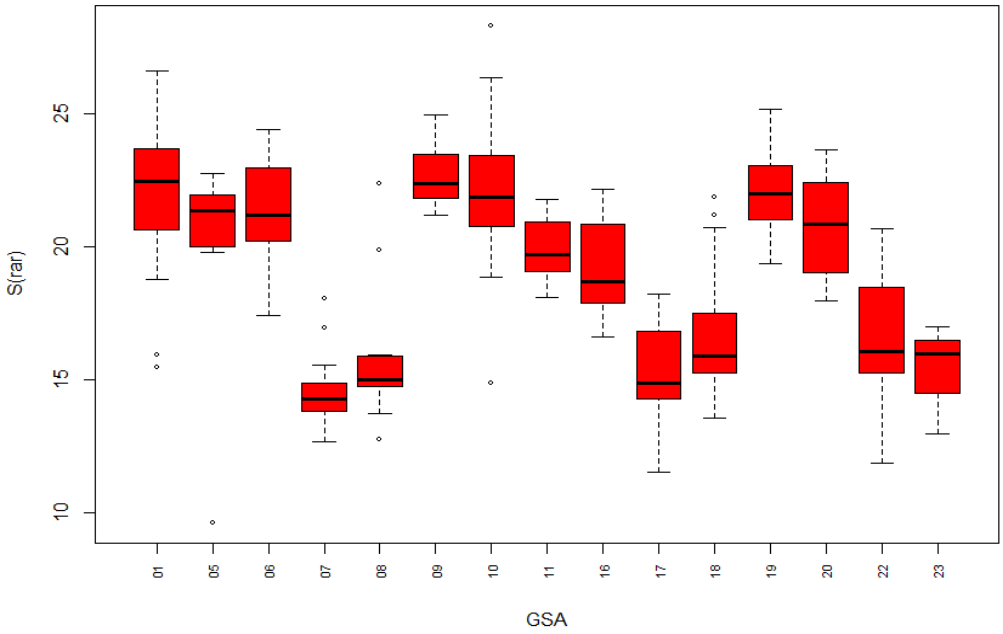



Figure 3.6: Species richness per GSA rarefied to 20 hauls. Samples included from 1994-2012.

The mean diversity and species richness over the whole Mediterranean did not show any temporal trend during the study period (1994-2012), with mean H' ranging between 0.81 and 0.94 and mean S between 3.8 to 4.5 species per haul (Fig 3.7). The lack of consistent temporal trends of H' and S also applied to regional level (Fig 3.8; as H' and S displayed a very similar pattern, only H' is shown). The absence of significant cross-correlations among temporal variation of H' indices of different areas (with the exception of the Adriatic with the Strait of Sicily time series, p=0.0238) evidences the general absence of synchronic behavior.

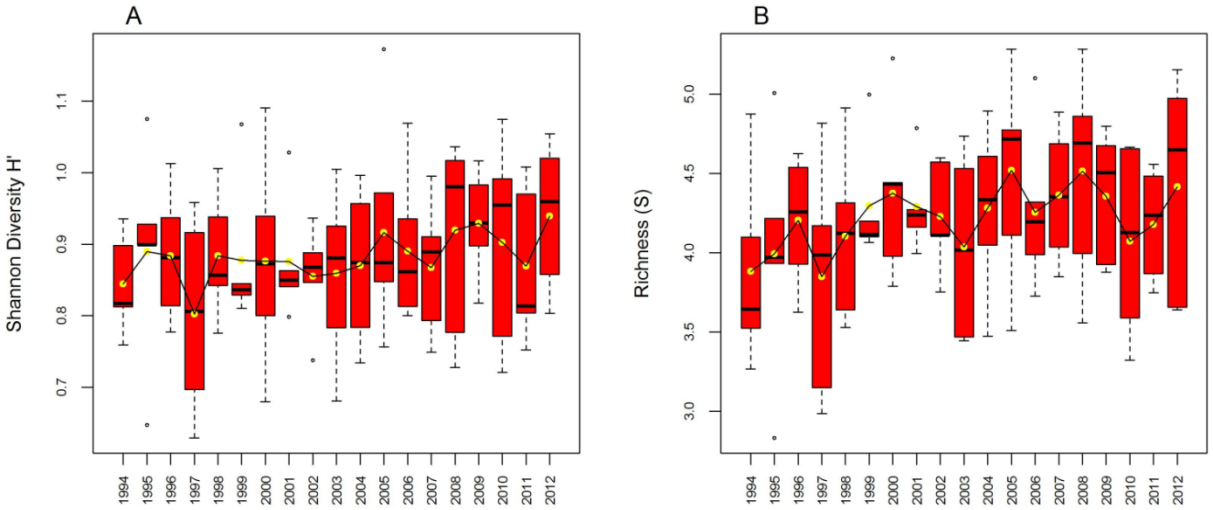



Figure 3.8: Boxplots of Shannon diversity (A) and Species richness (B) per haul, obtained using all MEDITS samples taken during 1994-2012.

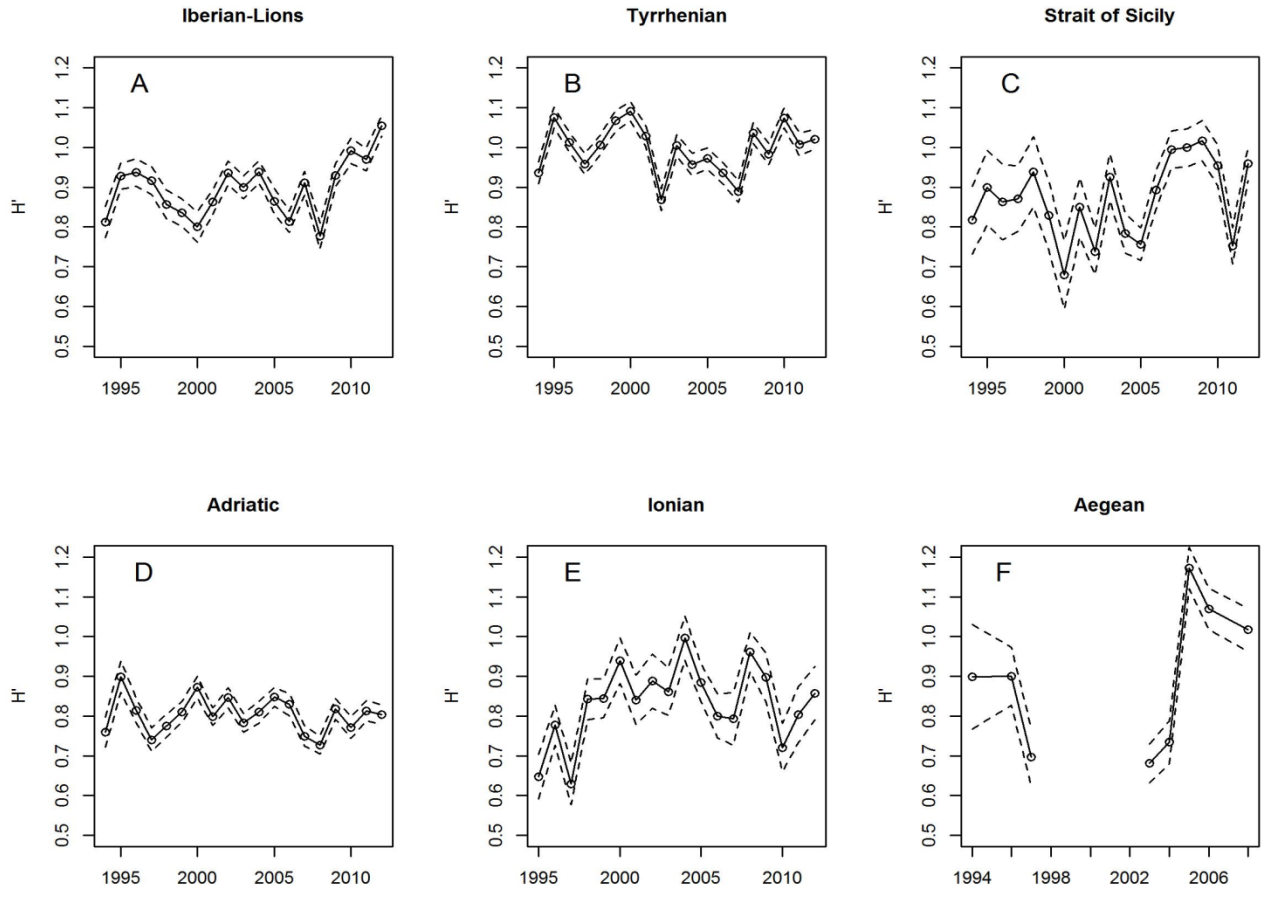



Figure 3.7: Temporal patterns of the Shannon diversity H' at six different Mediterranean bioregions using the MEDITS sampling carried out during 1994-2012.

### 3.4.2 Environmental drivers

The best models for H' and S were obtained including the factor year, a two-dimensional smoother for longitude and latitude, a depth-region interaction term, and smoothers for Chla and SST (Table 3.2). The depth-region interaction term indicates that the bathymetric pattern of diversity varies with the bioregion considered. The best fits for both models (H' and S) were obtained using the Chla of the winter preceding the sampling season. Regarding the SST, the best models for H' included the SST values of previous winters, while the richness model performed better using the spring SSTs. The deviance explained was much higher for the S model (35.9%) than the H' model (18.5%).

Table 3.2: Best model selection for H' and S based on explained variance, GCV and AIC. All variables shown in the model formulations were significant. Best model marked in bold.

| No | Model | R2 | GCV | k | AIC |
|---|---|---|---|---|---|
| 1 | H' ~ Year +Region +s(lat, long)+ depth | 15.8 | 0.1809 | - | 7079 |
| 2 | H' ~ Year +s(lat, long)+ depth * region | 18.2 | 0.1763 | - | 6917 |
| 3 | H' ~ Year +s(lat, long)+ depth * region + s(Chl Spring) + s(SST Spring) | 18.3 | 0.1763 | K=4/4 | 6916 |
| 4 | H' ~ Year +s(lat, long)+ depth * region + s(Chl Spring) + s(SST Winter) | 18.4 | 0.1758 | K=4/4 | 6901 |
| 5 | H' ~ Year +s(lat, long)+ depth * region + s(Chl Winter) + s(SST Spring) | 18.5 | 0.1758 | K=4/4 | 6899 |
| **6** | **H' ~ Year +s(lat, long)+ depth * region + s(Chl Winter) + s(SST Winter)** | **18.5** | **0.1757** | **K=4/4** | **6897** |

Modeling H', the partial effect of factor year was quite stable over the time series analyzed, with the only exception of 2007, whereas it varied without any clear trend for S (Fig 3.9). The spatial analyses (two-dimensional smoother for longitude and latitude) revealed slightly contrasting patterns between diversity and species richness (Fig 3.10). Overall, H' is high in the western Mediterranean basin including the Tyrrhenian and Alboran Seas, the waters around Sardinia and the Strait of Sicily. However, there is an area of comparatively low diversity values in the eastern coast of the Iberian Peninsula around the Ebro river mouth. Regarding the eastern basin, the Adriatic and Southern Aegean Seas have moderate and high H' values, whereas the waters around Crete showed the lowest values. Species richness was also high in the whole western basin, including the area around the Ebro mouth. In the eastern basin, S was high in the Ionian Sea and in the western part of the Southern Aegean; it was comparatively low in the northern and southern Adriatic Sea and around Crete. Overall, no consistent pattern in diversity and species richness were found along the Mediterranean.

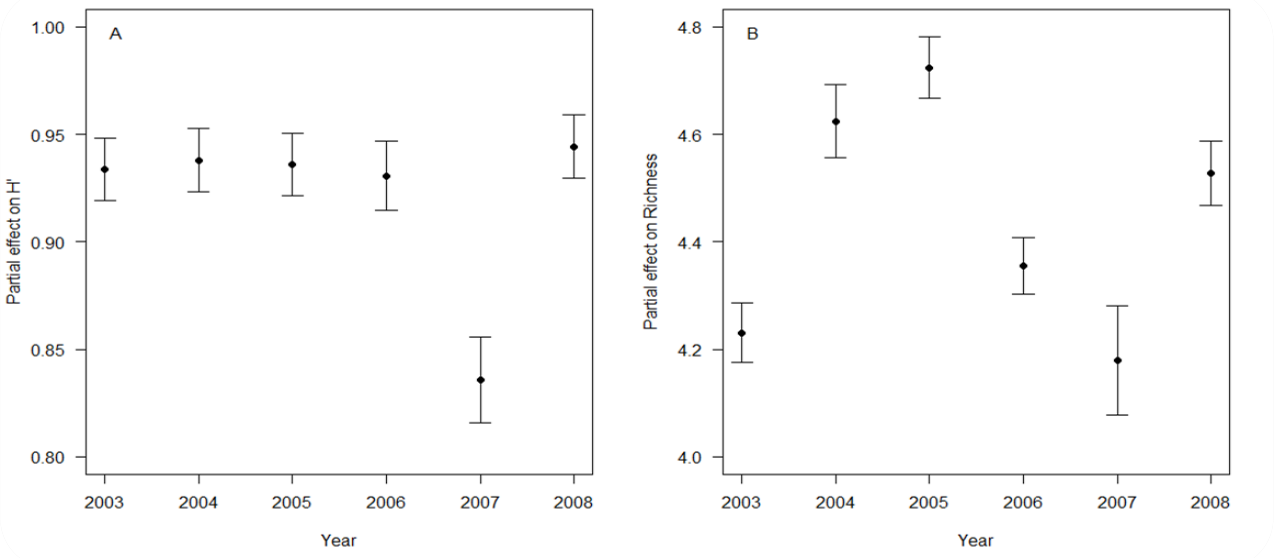



Figure 3.9 : GAM outputs for partial effects for factor "year" (mean ± S.E.) on Shannon diversity (A) and species richness (B) of Mediterranean cephalopods collected during MEDITS sampling (2003-2008).

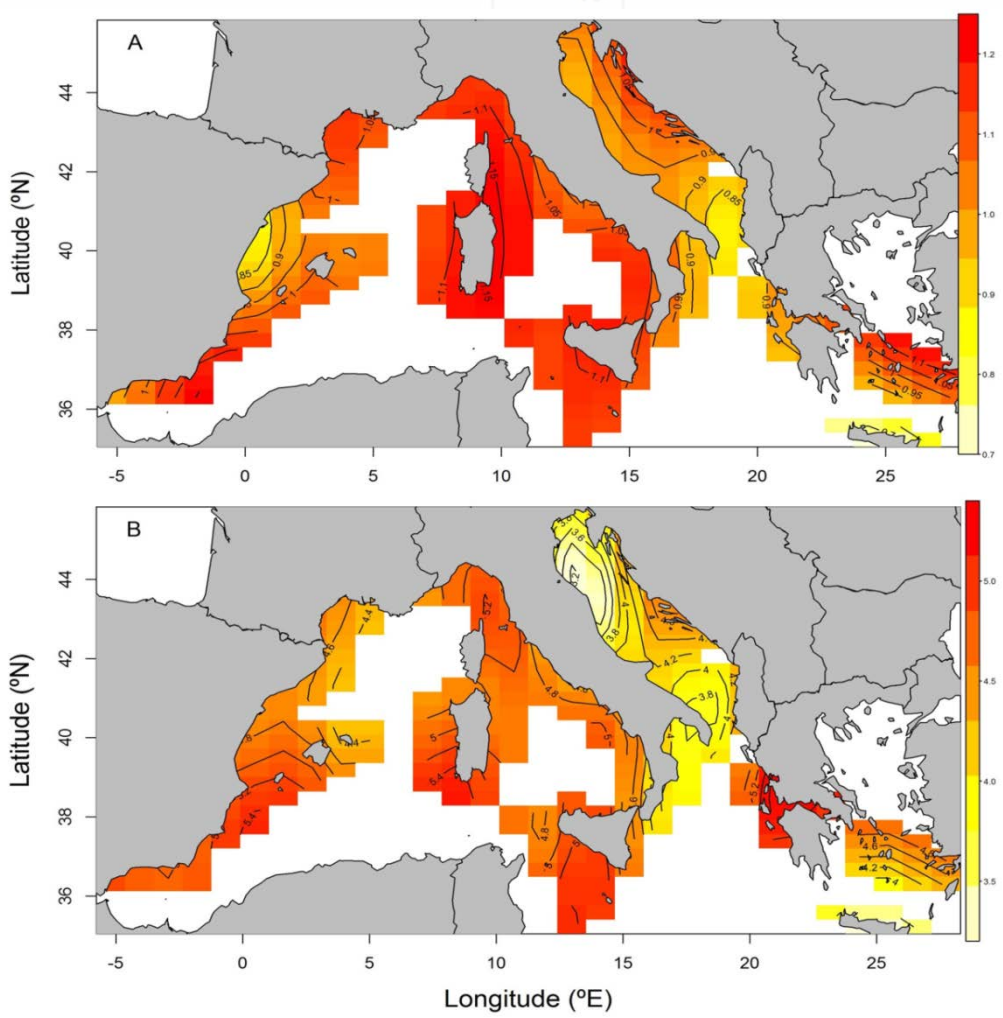



Figure 3.10: Spatial pattern of Shannon diversity H' (A) and species richness S (B) across the Mediterranean Sea as predicted by the GAM model.

The remaining variables analysed (depth, Chla and SST) displayed similar trends for H' (Fig 3.11) and S (Fig 3.12). The smoothers for depth were humpback shaped in the Iberian-Lions, Tyrrhenian and Ionian Sea, with maxima at 200 – 250 m in the two former regions and 300 m in the last one. In the Strait of Sicily and Aegean Sea, the effect decreased with depth but with a plateau at 100-400 m in the Strait of Sicily. The Adriatic Sea showed a completely different pattern, with a general increase with depth (punctuated with local maxima at about 100, 230 and 400 m depth) and a marked decrease in waters deeper than 400 m. In general, the strongest effect was found between 200 and 400 m depth, indicating that the highest diversity and species richness are likely to be found at the shelf break and upper slope.

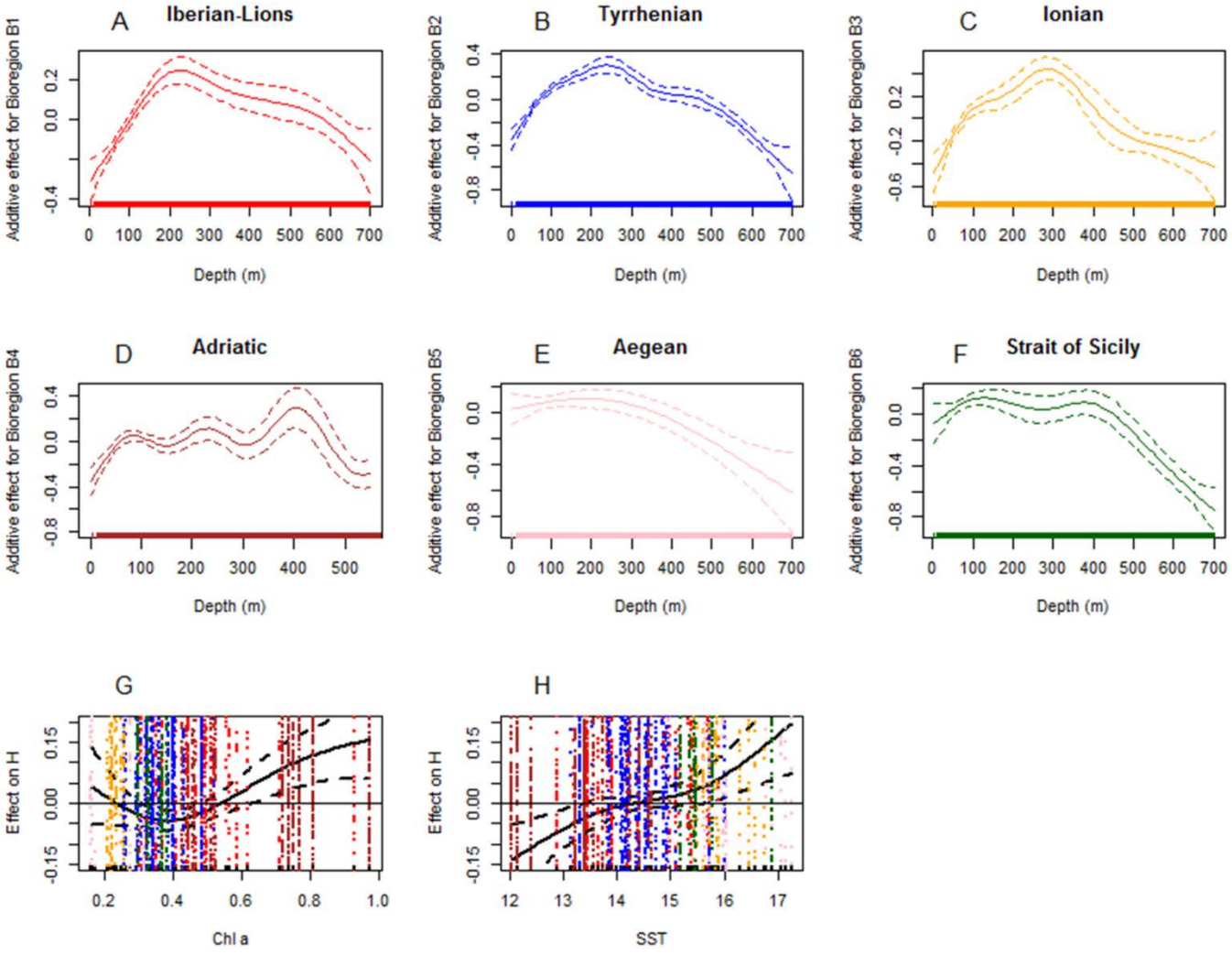



Figure 3.11: GAM outputs of partial effects for 1) depth at the six bioregions investigated (A-F), 2) chlorophyll concentration (Chla; G) and 3) surface sea temperature (SST; H) on Mediterranean cephalopod diversity H'. Solid lines indicate the fitted partial effects and broken lines the 95% confidence intervals (CI).

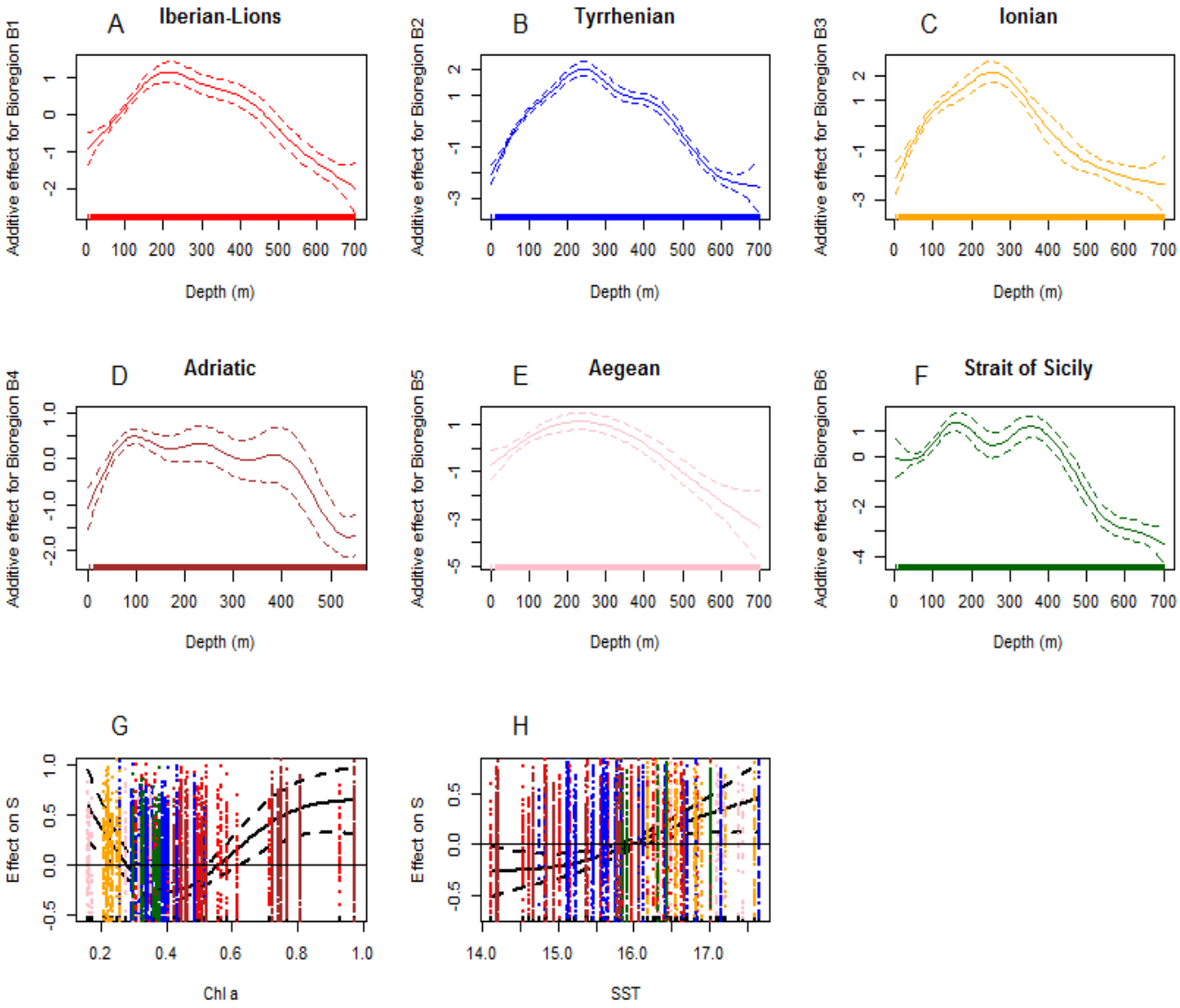



Figure 3.12: GAM outputs of partial effects for 1) depth at the six bioregions investigated (A-F), 2) chlorophyll concentration (Chla; G) and 3) surface sea temperature (SST; H) on Mediterranean cephalopod richness S. Solid lines indicate the fitted partial effects and broken lines the 95% confidence intervals (CI).

The effect of Chla on diversity took an inverted bell shape with diversity declining with increasing Chla content until the inflection point at values close to 0.4 mg·m-3 (Fig 3.11 G). After this point, diversity increased with increasing Chla. Partial residuals on the Chla effect indicates that the areas where Chla positively enhances diversity belong to the Southern Aegean Sea (pink dots) and the Adriatic (brown dots), which are the areas with the lowest and highest Chla respectively (Fig 3.11 G).

SST showed a general positive effect on diversity, with below-average diversity values at low temperatures (<14-16°C) and higher values at higher temperatures (Fig 3.11 H). The plotted partial residuals of the SST show that those below-average diversity values at high temperatures were mainly associated with the Strait of Sicily, the Ionian and the Aegean Sea (Fig 3.11 H), while the negative part of the SST effect was partially associated with the Adriatic and the Iberian-Lions area.

## 3.5 Discussion

The present study analysed spatio-temporal trends of cephalopod diversity in the whole Mediterranean Sea during the last two decades, using species richness and the Shannon-Wiener index as diversity descriptors. In spite of the intense sampling (18214 stations), the species accumulation curves did not level off in all areas, meaning that results should be carefully interpreted in a geographical context. Altogether 58 taxonomical units of cephalopods were found, of which 47 were determined to species level; these species account for 71% of the currently known Mediterranean cephalopod fauna (Bello, 2008).

Spatio-temporal patterns

The spatial distribution of cephalopod diversity showed no clear longitudinal or latitudinal gradients at the whole basin scale. This result is independent from the scale considered (haul, area) or the diversity measurement used (H', S), and differs from findings obtained analyzing unstandardized Mediterranean fish datasets (Quignard and Tomasini, 2000; Taviani, 2002; Ben Rais Lasram et al., 2009; Coll et al., 2010; Mouillot et al., 2011). Interestingly, the previous studies supporting a longitudinal trend of diversity are all based on data compiled from different data sources and cruises. On the other hand, a study on benthic Mediterranean deep-sea fauna combined different sampling programs with literature reviews and revealed that for most of the taxa analysed, a longitudinal gradient was only found regarding biomass and abundance, but not for diversity (Danovaro et al., 2010). These authors concluded that longitudinal trends are apparently weak and inconsistent across different components of deep-sea biota. In agreement with this, none of the three studies which analysed standardized large-scale, long-time Mediterranean datasets, namely on groundfish diversity (Gaertner et al., 2007, 2013) and fish diversity in general (Granger et al., 2015), found a clear spatial gradient of diversity. Instead they suggested that some areas in the eastern basin were much more diverse than previously thought. Granger et al. (2015) analyzed MEDITS data from 1994-2012 and found fish species richness per haul to be highest in the western areas of the western Mediterranean basin, in the eastern Ionian Sea, around Malta and in areas of the Aegean Sea. Gamma diversity, on the other hand, was lowest in the Adriatic but highest in the Balearic Sea, eastern Ionian Sea and the western part of the Southern Aegean Sea. Similar patterns were also found by Gaertner et al. (2007, 2013) for groundfish communities on the Mediterranean shelf and slope. In a former study, D'Onghia et al. (1996) already concluded that the North Aegean cephalopod diversity was as high as in any other Mediterranean area.

In spite of claims of biodiversity loss as a result of high anthropogenic impacts in the Mediterranean (fishing exploitation (Vasilakopoulos et al., 2014), pollution (Danovaro, 2003), climate change (Coma et al., 2009)), overall diversity of cephalopods has been rather stable over the last two decades. Such stability in species diversity with time also applies to fish (Granger et al., 2015). Consistent temporal trends were not found at regional scales either, as cephalopod diversity oscillated annually in a saw-tooth shape without any clear tendency. The only striking feature is the high diversity values in the Southern Aegean Sea during recent years, which seems not to be related to Lesseptian migrants (Golani, 1998) as our data contain no records of Red Sea species. The lack of

general trends in cephalopod and fish diversity during the last 20 years could be due to the fact that the ecosystem was already altered before the beginning of our time series or that noticeable changes will only be revealed at longer temporal scales.

Drivers of diversity

The diversity of Mediterranean cephalopods followed a hump-shaped bathymetric pattern, being highest between about 200-400 m, which is in accordance with previous works on cephalopod assemblages in the area. However, additional bioregion-dependent bathymetric patterns were observed. In the central Mediterranean, species richness increased with depth up to a peak at about 200 m and then decreased down to 600 m depth (Colloca et al., 2003). In the western basin, both species richness and diversity were highest on deep shelf and upper slope grounds between 100-600 m compared to shallower (50-100 m) and deeper (600-800) waters (Quetglas et al., 2000). A similar diversity pattern of decreasing species richness with depth at the whole Mediterranean scale was found for groundfish slope (>200 m) communities (Gaertner et al., 2013). However, bathymetric patterns in this work varied according to the type of diversity index used, e.g. an opposite relationship was found between taxonomic distinctness and depth. In the California current, by contrast, the use of the distinctness index also revealed the hump-shaped pattern (Tolimieri and Anderson, 2010).

The observed diversity patterns could be related to the so-called mid-domain effect, which states that diversity in a bounded geographical domain is highest in the middle of that domain. The mid-domain peak is independent from environmental gradients and only due to the maximum overlap of species distribution ranges at that point (Colwell and Lees, 2000). However, when testing this hypothesis with fish data from different regions, Kendall and Haedrich (2006) results did not tally with the mid-domain effect theory. Rosa et al. (2008a) came to the same conclusion in their study of large scale patterns in pelagic cephalopod diversity worldwide. Their study demonstrated highest diversity in the first 200 m but no evidence of the mid-domain effect. According to Levin et al. (2001), the hump-shaped form might result from optimal conditions (e.g. productivity) near the shelf-break; these systems are more productive and diverse habitats, often dominated by complex biocenoses (Colloca et al., 2004). Enhanced phytoplankton and zooplankton productions associated with shelf-break fronts have been observed in many ecosystems, and nurseries of numerous species are associated to shelf-break habitats in the Mediterranean (Mann and Lazier, 1996; Bartolino et al., 2008; Colloca et al., 2015). Differences in the extension and morpho-geographical characteristics of shelf-break habitats might be responsible for the different bathymetric effects evidenced in the six bioregions investigated.

Productivity has often been proposed to influence diversity, and various authors investigated this relationship. Our results indicate that low and high Chlorophyll *a* content (Chla) seems to enhance species diversity, as the GAM analysis showed a U-shaped effect with positive effect sizes associated with the Aegean and Ionian Sea on one hand (low Chla) and the Iberian-Lions and Adriatic regions (high Chla) on the other hand. This suggests that different mechanisms are in play in different areas, probably because the effect of productivity interacts with other factors and therefore depends on the ecosystem properties. The positive link between Chla content and diversity in productive areas could

be due to the fact that sufficient food resources enable less competitive species to survive better than in resource-limited environments, resulting in a higher evenness of the community (Rosa et al., 2008a, 2008b). Furthermore, more productive systems support more species and trophic levels (Dodson et al., 2000). In fact, a positive relation between net primary production and pelagic cephalopod diversity was found analyzing large-scale patterns worldwide, though this relation was very weak in coastal ecosystems (Rosa et al., 2008a, 2008b). For bacteria, there is experimental evidence showing that seasonal fluctuations in availability of limiting resources can favor biological diversity by the coexistence of different ecotypes via frequency dependent competition (Spencer et al., 2007). Based on regression analyses, McClatchie et al. (1997) found a relationship between demersal fish diversity and surface phytoplankton biomass, but they state that this effect may not be causal. A negative effect of Chla, as seen in areas of intermediate Chla content, could be explained by the rise of a few dominant species or changes in food quality (a different phytoplankton community composition having consequences on higher trophic levels) (Dodson et al., 2000). However, high diversity values observed in the less productive areas of the Mediterranean were likely related to different ecological processes. We argue that high diversity in rather oligotrophic and warm areas, such as the eastern Ionian and the Aegean Sea, may result from closer coupling of the cycles of primary and secondary producers and the low seasonal amplitude of these cycles (Rosa et al., 2008a). These characteristics of oligotrophic regions favor diversity (Longhurst and Pauly, 1987; Spencer et al., 2007). An additional explanation is that the contribution of different species of cephalopods to community diversity in the Eastern Mediterranean is likely different, with higher contribution of species less sensitive to primary production variability and higher sensitivity to other environmental variables, for example temperature (Fig 3.11 H) or rainfall (Lefkaditou et al., 1998). A recent studies in the Western Mediterranean shows that, on a given area, two cephalopods species display contrasting responses to a given environmental variable (Puerta et al., 2015).

Temperature is another parameter considered to influence species diversity via different pathways like biochemical rates, mutation rates or lifestyles (Rosa et al., 2008a). In contrast with a previous work carried out in the western Mediterranean (González and Sánchez, 2002), which did not find any relationship between temperature and cephalopod diversity, our analysis revealed a positive correlation between these parameters, the effect being stronger for S than for H'. A positive correlation with S was also found in a work of Ben Rais Lasram et al. (2009) comparing fish diversity in the whole Mediterranean with the mid-domain effect hypothesis (Ben Rais Lasram et al., 2009). In the Barents Sea, Johannesen et al. (2012) found contrasting results depending on the diversity index used, since the sea surface temperature (SST) – diversity correlation was negative and positive using H' and S, respectively. Changes in temperature may yield competitive advantages to certain species due to their higher temperature tolerances and/or mobility, which may lead to changes in species turnover and community composition (Siddon et al., 2011). Apparently, warmer SST leads to higher species number (Johannesen et al., 2012, this study), while the evenness can be affected either positively (this study) or negatively (Johannesen et al., 2012). Species dominance may be a context-dependent question related to the community composition and ecosystem characteristics.

Apart from the drivers analyzed in our study, there are other factors influencing species diversity. The geographical effect included in our models may capture some of these effects not explicitly included, such as the influence of the shelf area extension due to its importance as nursery areas. In previous studies, for instance, topographic features were found to affect fish (McClatchie et al., 1997) and cephalopod diversity (Krstulovic Sifner et al., 2005). Diversity patterns of different deep-sea taxa were found to vary according to the system (e.g. slope, canyon, sea mount), evidencing the importance of topographic and ecological features (Danovaro et al., 2010). Other studies reported that diversity depends on climate and shelf area, and gradients seem to be set by historical, geological and climatic events, external forcing and oceanographic boundaries rather than by the physiological response of organisms to climate (Rosa et al., 2008b; Ibáñez et al., 2009). The phenology of primary producers and how biological processes are coupled to them (e.g. diurnal, ontogenetic and reproductive migrations) would also be related to the spatial and temporal patterns observed (D'onghia et al., 1996). Furthermore, climate change and human induced perturbations such as fishing exploitation and habitat pollution can cause important impacts on marine biodiversity (Coll et al., 2012).

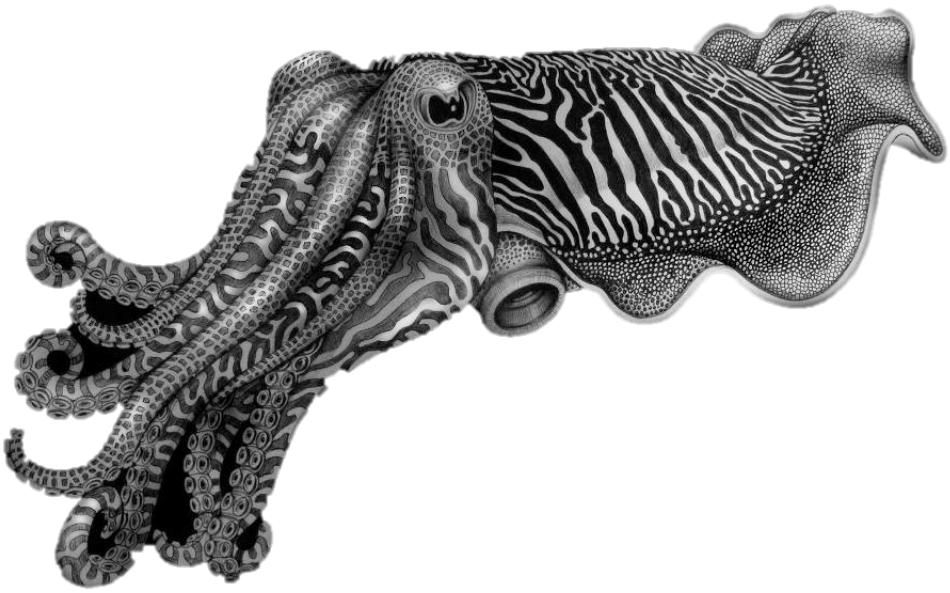
Diversity and climate change

According to the fifth report of the Intergovernmental Panel on Climate Change (IPCC) about progression and consequences of the climate change, temperature and precipitation will modify present regional climates. The observations show a clear increase in the temperature of the Earth's surface and the oceans. With the described and forecasted changes in temperature, salinity, pH, nutrients and oxygen, it is likely that Chla concentration will be altered simultaneously. According to the report, oligotrophic provinces already expanded at average rates of 0.8 to 4.3% per year between 1998 and 2006, probably due to the reduction in nutrient availability owing to increased stratification of water masses. Given the relationship between cephalopod diversity, SST and productivity, ongoing climate change will probably lead to changing spatial and temporal diversity patterns of these species (Zeidberg and Robison, 2007; Puerta et al., 2014). While expected raising temperatures might favour an increase in species richness according to our models, the effect of changed Chla concentration might depend on the specific bioregion. With the expected decrease of Chla concentration, diversity might decrease in less oligotrophy areas like the Adriatic Sea and the Iberian-Lions region (situated on the right part of the U-shaped Chla effect), while according to our model an increase in diversity would be possible in the Aegean Sea, the Ionia Sea and in some areas of the Strait of Sicily. However, according to different climatic models of a study of Macias et al. (2015), these regions are more likely to experience an increase in Chla rather than a decrease, due to vertical density changes caused by a combination of warming and salinization. According to our model, diversity would therefore decrease in these areas as well.

## 3.6 Conclusion

Our study, based on a standardized long-term Mediterranean-scale survey dataset, presents spatio-temporal patterns of cephalopod diversity measured by two different diversity indices. Cephalopod diversity showed no clear longitudinal or temporal trends over the last two decades. The spatio-temporal pattern of cephalopod diversity in the

Mediterranean seems to be driven only partly by temperature and productivity gradients, as local physical and geographical factors like depth appear to be of influence as well. A useful expansion of the present study could be the integration of biotic factors (e.g. species aggregation, competition) as well as anthropogenic influences like pollution or fishing pressure (Granger et al., 2015). Together with previous studies on fish diversity, the present results are of paramount importance to be used as a baseline scenario for future analyses of Mediterranean biodiversity over the next decades, such as the one foreseen by the European Marine Strategy Framework (Directive 2008/56/EC).



# Chapter 4

# Environmentally driven synchronies of Mediterranean cephalopod populations

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# Environmentally driven synchronies of Mediterranean cephalopod populations

## 4.1 Abstract

The Mediterranean Sea is characterized by large scale gradients of temperature, productivity and salinity, in addition to pronounced mesoscale differences. Such a heterogeneous system is expected to shape the population dynamics of marine species. On the other hand, prevailing environmental and climatic conditions at whole basin scale may force spatially distant populations to fluctuate in synchrony. Cephalopods are excellent case studies to test these hypotheses owing to their high sensitivity to environmental conditions. Data of two cephalopod species with contrasting life histories (benthic octopus vs nectobenthic squid), obtained from scientific surveys carried out throughout the Mediterranean during the last 20 years were analyzed. The objectives of this study and the methods used to achieve them (in parentheses) were: i) to investigate synchronies in spatially separated populations (decorrelation analysis); ii) detect underlying common abundance trends over distant regions (dynamic factor analysis, DFA); and iii) analyse putative influences of key environmental drivers such as productivity and sea surface temperature on the population dynamics at regional scale (general linear models, GLM). In accordance with their contrasting spatial mobility, the distance from where synchrony could no longer be detected (decorrelation scale) was higher in squid than in octopus (349 vs 217 km); for comparison, the maximum distance between locations was 2620 km. The DFA revealed a general increasing trend in the abundance of both species in most areas, which agrees with the already reported worldwide proliferation of cephalopods. DFA results also showed that population dynamics are more similar in the eastern than in the western Mediterranean basin. According to the GLM models, cephalopod populations were negatively affected by productivity, which would be explained by an increase of competition and predation by fishes. While warmer years coincided with declining octopus numbers, areas of high sea surface temperature showed higher densities of squid. Our results are relevant for regional fisheries management and demonstrate that the regionalisation objectives envisaged under the new Common Fishery Policy may not be adequate for Mediterranean cephalopod stocks.

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## 4.2 Introduction

The Mediterranean Sea is generally shaped by large scale gradients of temperature, productivity and salinity (D'Ortenzio and d'Alcalá, 2009). However, it is also known as a complex ecosystem with contrasting regions in terms of productivity (Nieblas et al., 2014), seafloor topography and hydrography (Millot, 2005; Rossi et al., 2014). In an ecosystem with such pronounced regional differences, animal populations are prone to exhibit patchy distributions due to different habitat conditions. Such patchiness has been observed analysing feeding habitats of high trophic level species such as whales and tuna (Druon et al., 2011, 2012, 2016), the distribution of secondary

consumers such as cephalopods or small elasmobranchs (Puerta et al., 2015, 2016a; Navarro et al., 2016) or nursery grounds and spawning areas of commercially important species (Druon et al., 2011, 2015; Colloca et al., 2015). All these studies revealed that hydrographic conditions (Druon et al., 2011, 2015), bathymetric features like depth and type of seafloor (Druon et al., 2012; Colloca et al., 2015) and productivity (Druon et al., 2011, 2012; Puerta et al., 2016a) are key drivers of distribution patterns.

Environmental and large-scale climatic variability may force spatially distant populations to fluctuate in synchrony (Liebhold et al., 2004). Comparing the dynamics of spatially distant populations allows detecting the main drivers of abundance fluctuations and the scale at which they operate (Descamps et al., 2013), and thus the degree of connectivity of neighbouring populations. In synchronized populations, drastic declines in population size likely affect all populations simultaneously, exposing them to a greater risk of extinction (Descamps et al., 2013 and references therein). By contrast, heterogeneous and complex populations generally show higher resilience and recovery rates and are more likely to withstand mass elimination (Schindler et al., 2010). Therefore, knowledge about the underlying mechanisms of population dynamics at large spatial scales has important implications for the management and conservation of species (Liebhold et al., 2004).

Large-scale synchronic fluctuations have been described in phytoplankton (Doyle and Poore, 1974), zooplankton (Batchelder et al., 2012), fish (Kelly et al., 2009) and crustaceans (Koeller et al., 2009; Hidalgo et al., 2015). However, very little is known about cephalopods. This group is considered excellent for case studies to analyze synchronic fluctuations, owing to its sensitivity to changing environmental conditions as a result of its fast growth rates and short life cycles (Pierce et al., 2008). Among the environmental parameters investigated until now, sea surface temperature (SST) plays an important role in driving cephalopod abundance trends (Zuur and Pierce, 2004; Chen, 2010). Additionally, a recent study investigated local scale seasonal synchronies in Mediterranean cephalopod abundances (Puerta et al., 2016b), revealing contrasting seasonal cycles in response to local environmental conditions.

Due to the decline in the traditional finfish resources, European cephalopod fisheries, which were once located mostly in the Mediterranean, have grown and expanded northwards (Pierce et al., 2010). This expansion is expected to continue as a result of the increasing market demand of cephalopods, whereby regular assessments and certain management measures would be needed to ensure a sustainable exploitation. Under the current Common Fisheries Policy (CFP; EU Regulation Nº 1380/2013), the regionalization approach may lead to a revision of the management areas currently in place in the Mediterranean (see below). For a successful implementation, gaining knowledge of the mechanisms controlling stock fluctuations is essential, as defining management areas merging independently fluctuating populations may result in strong miss-management. Sound scientific knowledge is necessary to implement management areas appropriately matching the biological distribution of populations as demanded by the new CFP in their regionalised ecosystem-based approach.

Here we analyse the population dynamics of two commercially important cephalopods (Sartor et al., 1998; Quetglas et al., 2000) with contrasting life histories, the nectobenthic broadtailed shortfin squid *Illex coindetii* and the benthic common octopus *Octopus vulgaris,* in the whole Mediterranean Sea. The data analysed were obtained from scientific surveys carried out throughout the Mediterranean during the last 20 years. The objectives of this study are three-fold. For each species, we first analyse the global correlation structure across the entire Mediterranean Sea to assess how the similarity in population abundances of spatially separated populations (or population sub-units) decreases with distance. Second, we use dynamic factor analysis to detect underlying common abundance trends over distant regions. Finally, we analyse putative influences of key environmental drivers (productivity and SST) on the population dynamics at regional scale using general linear models.

## 4.3 Material and methods

### 4.3.1 Data source

Data were obtained from the international Mediterranean bottom trawl survey MEDITS (http://www.sibm.it/MEDITS%202011/principalemedits.htm), which is conducted every year in spring / early summer (May-August) since 1994, covering depths from 10 m down to 800 m. The surveys are performed by all riparian EU countries, in addition to Montenegro and Albania, and are the most comprehensive data sources to investigate demersal ecosystems in the entire Mediterranean. The sampling methodology is standardized among all the countries (for details see Bertrand et al., 2002 and A.A.V.V., 2016). A stratified random sampling design is used for this survey, with bathymetric strata comprising 10-50, 51-100, 101-200, 201-500 and 501-800 m. The standardized gear used is a GOC 73 trawl with a cod-end mesh size of 20 mm and a vertical and horizontal opening of the net of about 2 m and 18 m respectively (Bertrand et al., 2002). The net opening is measured by an attached underwater Scanmar or SIMRAD system, which allows calculating the swept area. Trawling is conducted during daylight, with a towing speed of about 3 knots and haul duration of 30 and 60 minutes over shelf and slope grounds respectively. Haul catches are sorted to species level whenever possible. Abundance data for each species are standardized to number of individuals per $km^2$ using the mean stratified swept area method (Saville, 1977; Souplet, 1996). Mean abundances per GSA were then obtained taking into account only the strata where 95% of the catches occurred, and including all valid hauls of these strata.

The geographical sub-areas (GSA's; Fig 4.1) established by the General Fisheries Commission for the Mediterranean (http://www.fao.org/gfcm/en/) for assessment and management have been used as spatial units in the present study. Some areas sampled only in recent and/or very few years were excluded from these analyses (GSA 2, 15 and 25). Although Greece did not conduct the surveys in 2007 and 2009-2012, its data were included as they represent the easternmost data points of the time series. The final dataset included 15 GSAs and comprised between 13 and 20 years depending on GSA. In total, 20463 hauls were analysed.

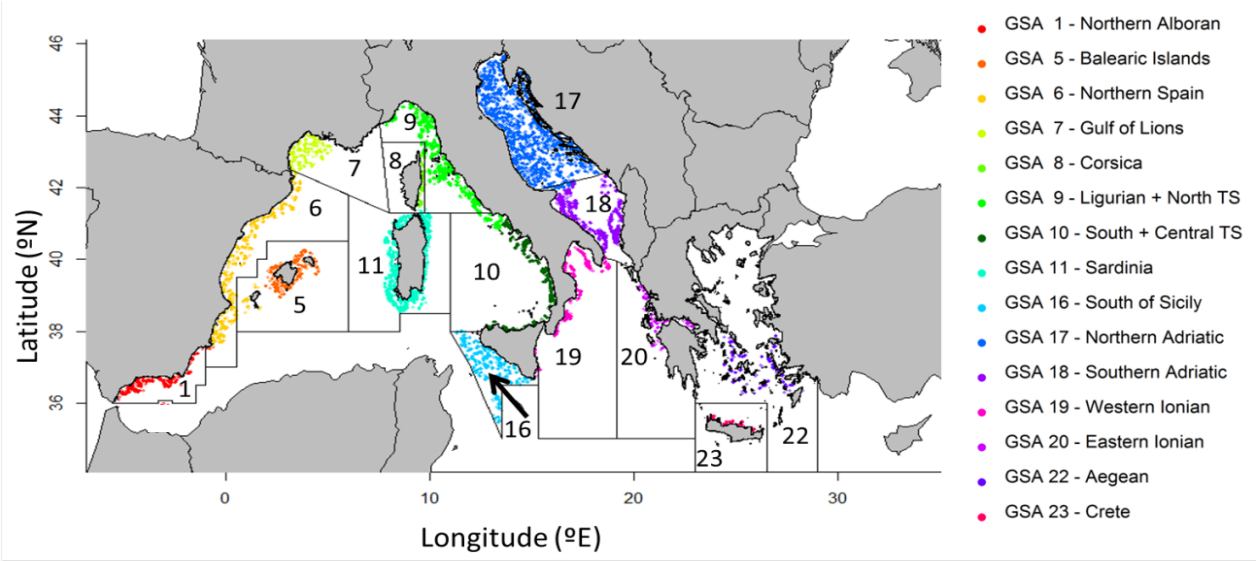



Figure 4.1: Map of the Mediterranean Sea showing the geographical sub-areas (GSAs) established by the General Fisheries Commission for the Mediterranean (GFCM) and the MEDITS stations sampled during 1994-2013.

### 4.3.2 Data analysis

#### 4.3.2.1 Decorrelation analysis

For both study species (*Octopus vulgaris* and *Illex coindetii*), the Pearson's correlation coefficient r was calculated for each pair of abundance time series and plotted against the distance between the GSAs' centres of gravity (Woillez et al., 2007). A centre of gravity is the mean location of an individual taken at random in the field, and discrete summation over sampling locations divided by population density gives the average location of a population in the respective sampling area. This method only takes into consideration positive records, that is sampling locations where cephalopods have been found (Woillez et al., 2007). To correct for differences in time series lengths, each coefficient was weighted by the length of the corresponding time series. The graphical output (spatial correlogram) shows the decline of synchrony with distance (Kelly et al., 2009) and the spatial scale of synchrony. The distance from where synchrony can no longer be detected is referred to as "decorrelation scale". Points were fitted by non-linear least squares estimation using an exponential fit:

$$q_d = q_0 e^{-d/v}$$

with $q_d$ being the Pearson's r correlation coefficient between CPUE time series of a pair of locations, $q_0$ the estimated correlation between CPUEs at zero distance, d stands for the distance between locations (km), and 1/v ($km^{-1}$; v > 0) is the decay rate that estimates spatial correlation scale as the e-folding scale of the exponential fit, i.e., the distance at which $q_d = e^{-1}$ (Kelly et al., 2009).

#### 4.3.2.2 Dynamic Factor Analysis (DFA)

To identify underlying common trends in abundance among time series, a Dynamic Factor Analysis (DFA, Zuur et al., 2003) was used. This technique can cope with non-stationary data, short time series and also missing values (Zuur et al., 2003), and has already been implemented for the identification of temporal trends of exploited species in various studies (Zuur et al., 2003; Erzini, 2005; Chen et al., 2008; Chen and Lee, 2013). DFA is a dimension reduction technique in which a set of time series are modelled as a linear combination of underlying common trends + factor loadings (+ covariates) + error terms to explain temporal variability. Factor loadings indicate how much each time series resembles each common trend. Covariates can be included, but only one yearly value per model. As this is not appropriate in a heterogeneous and extensive environment like the Mediterranean Sea, the effect of covariates will be unmasked separately by means of General Linear Models (see below). The correlation of observation errors can be modelled using different error matrices: i) same variance and no covariance (diagonal-equal); ii) different variances and no covariance (diagonal-unequal); iii) same variance and covariance (equalvarcov); and iv) different variances and covariances (unconstrained). For both species, the correlations of observation errors were fitted to all possible model structures in the time series, including 1 up to 3 common trends.

Owing to pronounced differences in environmental conditions (temperature, productivity regimes), oceanographic properties and hydrography between the western and eastern Mediterranean basins (Lascaratos et al., 1999), two separate DFA-analyses were conducted grouping GSAs according to their location. GSAs 1-16 are positioned in the western Mediterranean, while GSAs 17-23 are located in the eastern basin. In this analysis, we included time series of 13-20 years length from 15 different GSAs. For comparison, abundance data were scaled between 0 and 1.

The corrected Akaike information criterion (AICc) was used as a measure of goodness-of-fit, the best model having the lowest AIC (Zuur et al., 2003; Chen and Lee, 2013). All analyses were done in R (version 3.2.1; http://www.r-project.org/) using the Multivariate Autoregressive State-Space (MARSS) package (Holmes et al., 2012).

#### 4.3.2.3 General Linear Models

General Linear Models (GLM) were applied to investigate the influence of environmental drivers on the abundance of the two objective species. Sea surface temperature (SST) and chlorophyll *a* concentration (Chla) were used as putative drivers owing to their significant effects on cephalopod populations (Keller et al., 2014 / Chapter 5; Pierce et al., 2008b; Puerta et al., 2016b). Chla and SST data resulted from MODIS-Aqua and NPP-VIIRS sensors measurements already processed with regional ocean colour algorithms (resolution 1 km, daily data) and were downloaded from the MyOcean database (http://marine.copernicus.eu/web/69-interactive-catalogue.php). The availability of satellite data restricted this analysis to the time series of 1998-2012 from 15 GSA's. Available survey years per GSA reach from a minimum of 9 to a maximum of 15 years.

Cephalopod abundances (response variable) were modelled using the following explanatory variables: SST, Chla, year and GSA. Year and GSA were considered factors. Mean seasonal Chla and SST were averaged separately for each GSA for all years. Chla concentration was used as a proxy for food availability and was modelled using seasonal means of: i) the spring (March-May) before the survey, and ii) the preceding winter (December-February). By doing that we account for different time lags (time required for energy transfer between trophic levels), and also for the fact that food availability will influence ecological and metabolic processes differently across ontogeny. For this last reason, the same two seasons were used to calculate mean seasonal SST. Covariates (Chla, SST) and seasons (winter, spring) of year were chosen as they proofed to be good descriptors of the key oceanographic processes determining spring productivity in the Mediterranean (Lloret et al., 2001; Quetglas et al., 2011).

Two different models, designed for different purposes, were constructed for each species. The first one (non-standardized model) included the log of the catch per unit effort (CPUE) as response variable and attempts to detect proportional (temporal and spatial) effects between CPUE and environmental covariates:

Log (CPUE) ~ YEAR + GSA + Chla_Winter + Chla_Spring + SST_Winter + SST_Spring.

The second model (standardized model) was based on standardized data for CPUE, SST and Chla (data scaled between 0 and 1). This model is specifically designed to look at the influence of the covariates on the inter-annual variability once spatial gradients are removed, taking into account the interactions between SST/Chla and the GSAs to analyse regional-specific differences of environmental influences. This model therefore detects possible drivers for synchronic behaviour of spatially distant populations:

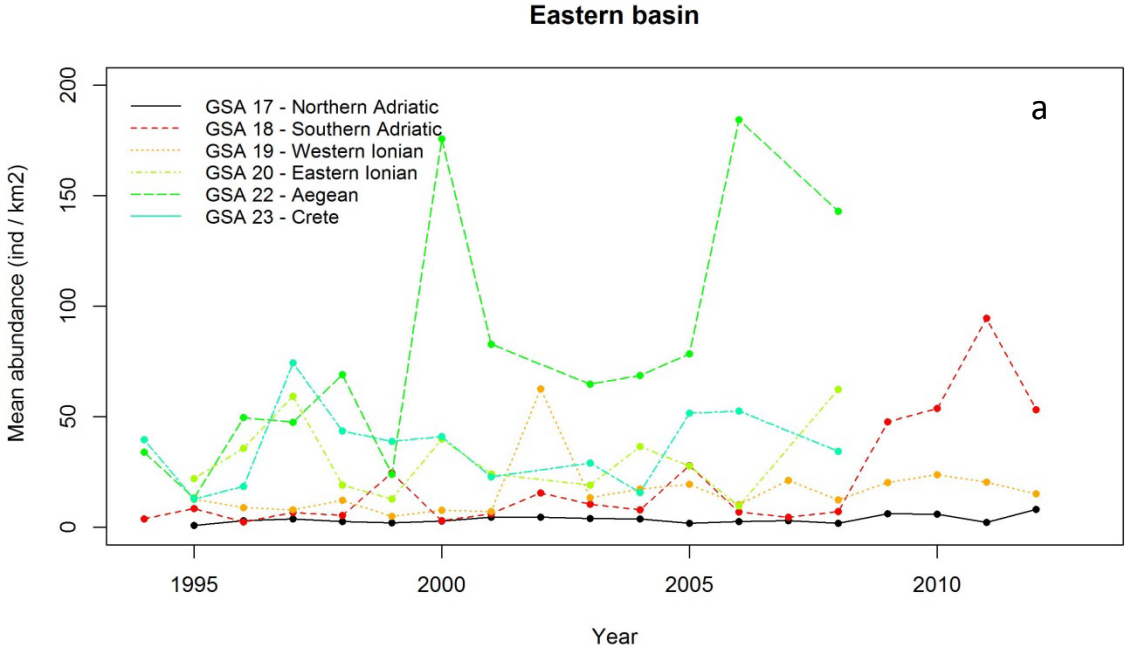
CPUE (standardized) ~ YEAR + GSA + Chla_Winter + Chla_Spring + SST_Winter + SST_Spring + Chla_Winter:GSA + Chla_Spring:GSA + SST_Winter:GSA + SST_Spring:GSA.

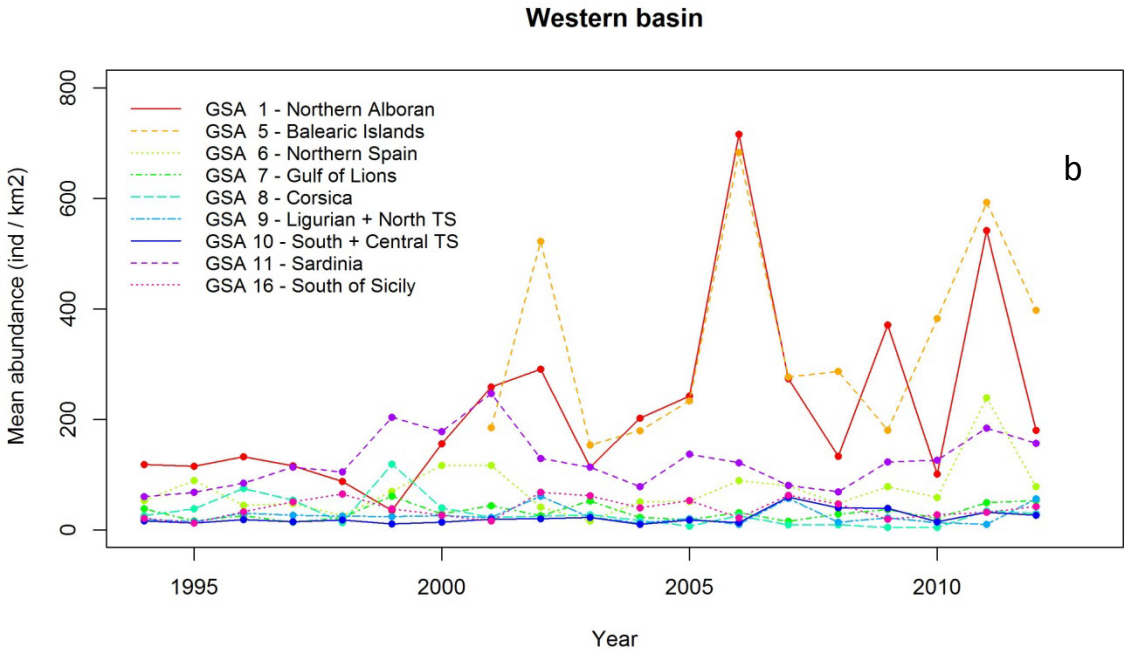
As spring and winter variables of Chl /SST were correlated, models with both spring and winter values of the same covariate were excluded. All GLM analyses were carried out with R (version 3.2.1, packages *mgcv* and *MuMln*) assuming Gaussian error distribution and using the identity link function. Models were selected according to their sample-size corrected Akaike Information Criterion (AICc), with the model resulting in the lowest value being considered the best fit (Burnham and Anderson, 2004). The variance inflation factor (VIF) was calculated for the best model to confirm the absence of correlation amongst covariates (VIF < 5). Model residuals were checked for variance homogeneity and normal distribution.

## 4.4 Results

### 4.4.1 Abundance data

CPUEs of *Octopus vulgaris* normally do not exceed 300 individuals/km², with the exceptions of the Alboran and the Balearic Sea, where the highest catches occurred (Fig 4.2 a + b). Except in the Northern Adriatic and western Ionian Sea (GSA 17, 19), CPUEs show an – often remarkable - increase in the year 2011. Octopus catches were generally higher in the western basin. The opposite is true for the *Illex coindetii* abundances, which are generally lower in the west (Fig 4.2 c + d). Squid CPUEs were highest in the waters around Crete (GSA 23), while lowest in the Gulf of Lions (GSA 7) and around the Balearic Islands and Corsica (GSA 5, 8), although the last two areas showed high abundances in some recent years. The high squid abundance in Northern Spain in 2000 was based on various high catches and is no outlier.



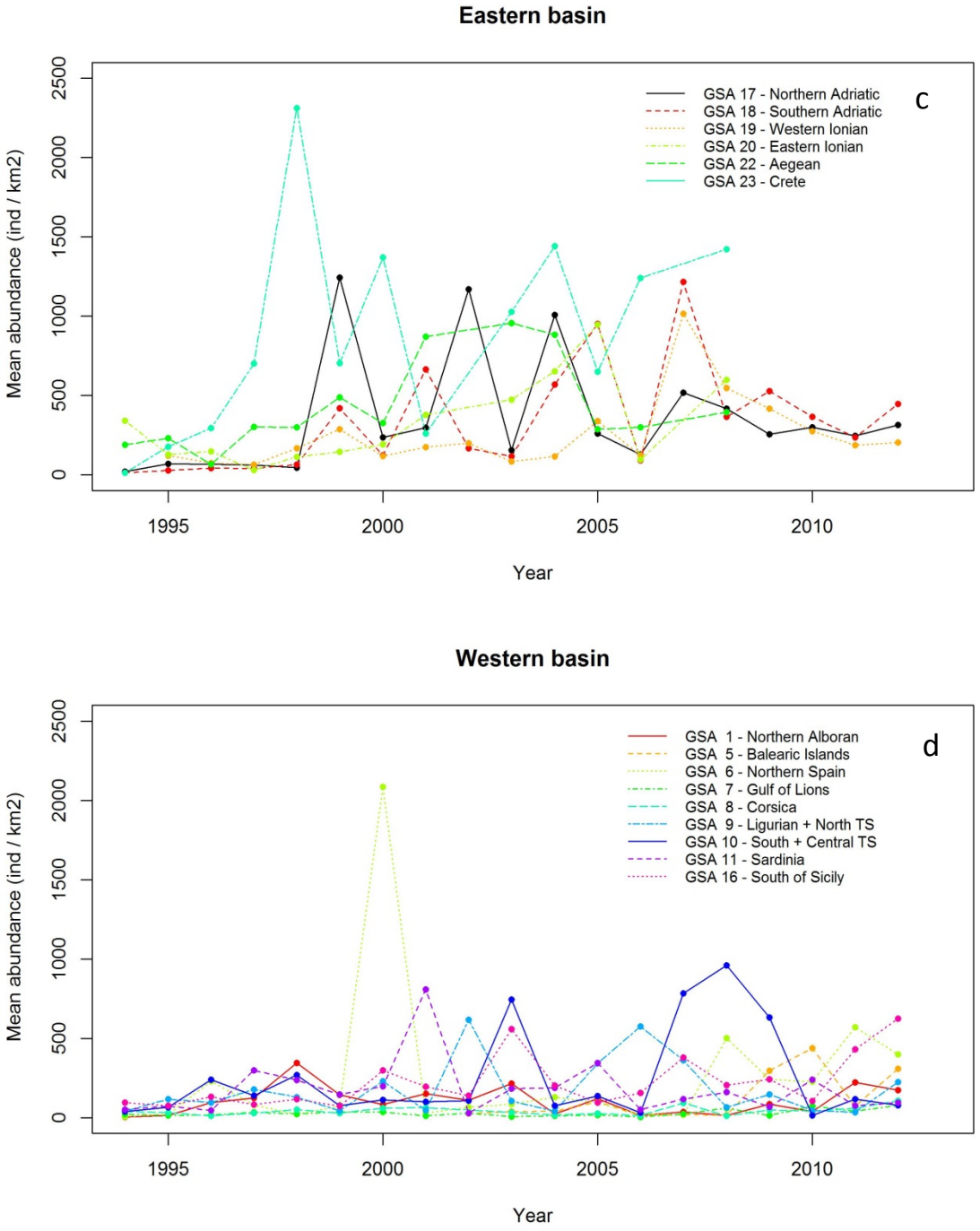



Figure 4.2: Time series of CPUEs (ind·km$^{-2}$) for *Octopus vulgaris* (a, b) and *Illex coindetii* (c, d) in the eastern and western Mediterranean basin from 1994 to 2012. TS = Tyrrhenian Sea

### 4.4.2 Decorrelation analysis

As expected, correlations between locations decreased with distance, describing a significant non-linear fit ($p<0.05$) for both species (Fig 4.3). The decorrelation scale was higher for squid (349 ± 43 km) than for octopus (217 ± 37 km). For comparison, the maximum distance between locations was around 2620 km.

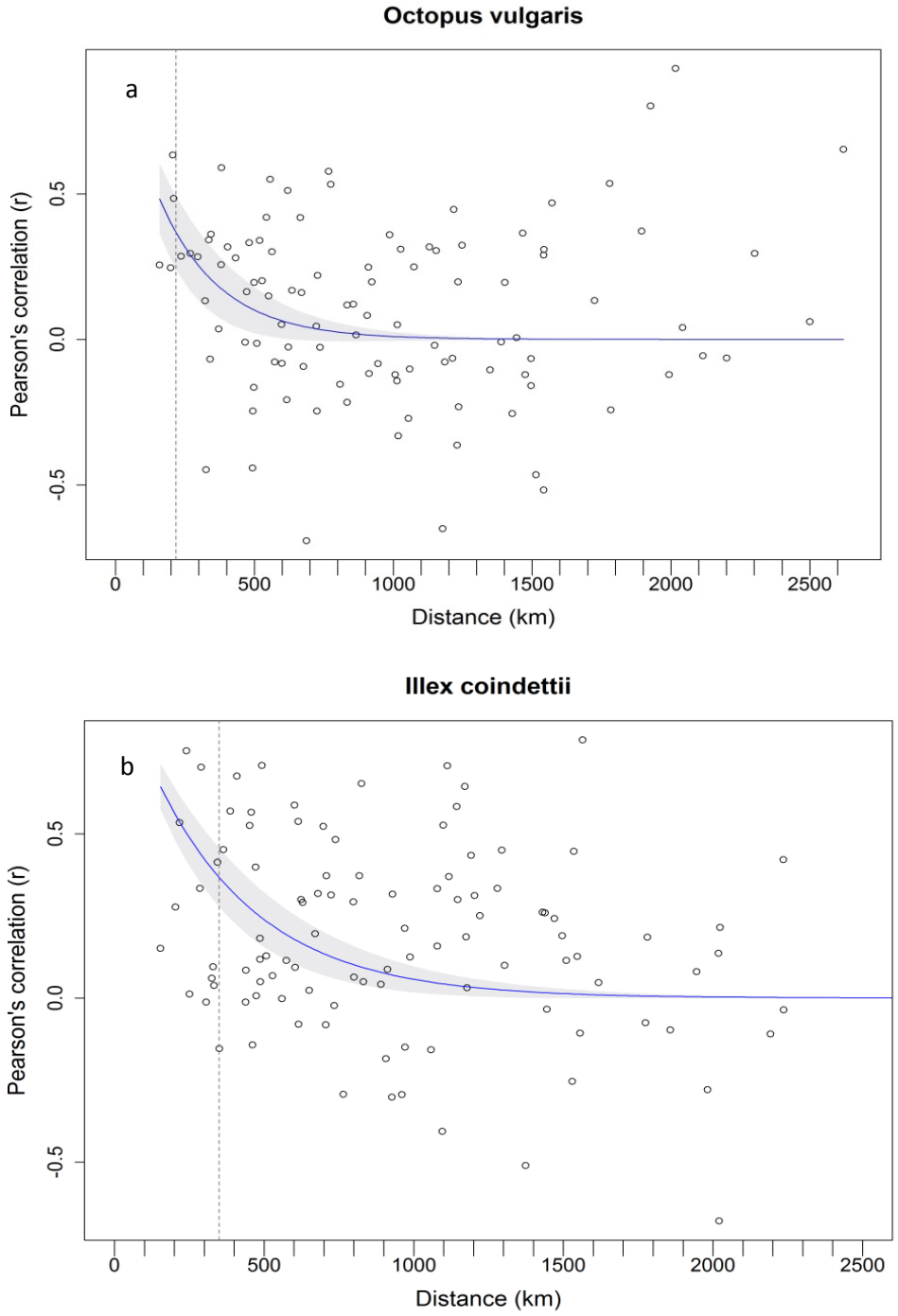



Figure 4.3: Correlograms of CPUEs of *Octopus vulgaris* (a) and *Illex coindetii* (b) showing the Pearson's correlation coefficients between all pairs of time series versus their distances. Model fits (least-square estimates, blue lines) and confidence intervals (in grey) are shown. Vertical lines indicate the spatial decorrelation scale.

### 4.4.3 Dynamic Factor Analysis

For both species and in both basins, the best DFA model had a single common trend and observation errors either with equal variances and no covariance (diagonal and equal) or equal variances and covariances (equalvarcov) (Table 4.1). All trends exhibit higher values in 2012 than at the start of the time series in 1994 (Fig 4.4). Furthermore, all trends show an increase in CPUEs during the last few years.

The common abundance trends for octopus show a steady rise in the eastern basin and a slightly time-delayed rise in the western basin, with abundances increasing continuously only from 1999 onwards. The factor loadings reveal that octopus abundances follow the common rising trend in all areas (Fig 4.4 b) in the eastern basin and in most areas in the western basin, with the exception of the waters around Corsica and south of Sicily (GSAs 8 and 16, Fig 4.4 d).

Although squid abundances showed a general increasing trend with time on both basins (Fig 4.4 e+g), the western one was truncated with a small decrease during 2000-2006 (Fig 4.4 g). In the eastern basin, factor loadings of all areas were positive with no opposite trends (Fig 4.4 f). Factor loadings for the western basin show that the Tyrrhenian and the Ligurian Sea (GSAs 9 and 10) and the waters of Sardinia (GSA 11) follow abundance trends opposite to the common trend (Fig 4.4 h).

Table 4.1: DFA results for *Octopus vulgaris* and *Illex coindetii* from the eastern and the western Mediterranean basin. Shown are the twelve best models for each case (best model in bold). For each model, the model number, the error matrix structure (R), the number of common trends (m), and the corrected AIC (AICc) are given.

| *Octopus vulgaris* - Eastern Mediterranean | | | |
|---|---|---|---|
| MODEL | R | m | AICc |
| **1** | **diagonal and equal** | **1** | **267.56** |
| 7 | equalvarcov | 1 | 269.89 |
| 4 | diagonal and unequal | 1 | 275.40 |
| 2 | diagonal and equal | 2 | 279.59 |
| 8 | equalvarcov | 2 | 282.03 |
| 5 | diagonal and unequal | 2 | 288.72 |
| 3 | diagonal and equal | 3 | 290.76 |
| 9 | equalvarcov | 3 | 293.49 |
| 6 | diagonal and unequal | 3 | 301.44 |
| 10 | unconstrained | 1 | 307.26 |
| 11 | unconstrained | 2 | 337.45 |
| 12 | unconstrained | 3 | 358.44 |

| *Octopus vulgaris* - Western Mediterranean | | | |
|---|---|---|---|
| MODEL | R | m | AICc |
| **7** | **equalvarcov** | **1** | **475.39** |

| | | | |
|---|---|---|---|
| 1 | diagonal and equal | 1 | 476.96 |
| 8 | equalvarcov | 2 | 479.15 |
| 2 | diagonal and equal | 2 | 483.64 |
| 4 | diagonal and unequal | 1 | 490.29 |
| 9 | equalvarcov | 3 | 492.26 |
| 3 | diagonal and equal | 3 | 494.72 |
| 5 | diagonal and unequal | 2 | 495.58 |
| 6 | diagonal and unequal | 3 | 509.32 |
| 10 | unconstrained | 1 | 540.39 |
| 11 | unconstrained | 2 | 558.08 |
| 12 | unconstrained | 3 | 592.66 |

| *Illex coindetii* - Eastern Mediterranean | | | |
|---|---|---|---|
| MODEL | R | m | AICc |
| **7** | **equalvarcov** | **1** | **269.52** |
| 1 | diagonal and equal | 1 | 270.01 |
| 4 | diagonal and unequal | 1 | 277.11 |
| 8 | equalvarcov | 2 | 279.49 |
| 2 | diagonal and equal | 2 | 280.03 |
| 5 | diagonal and unequal | 2 | 283.67 |
| 9 | equalvarcov | 3 | 290.85 |
| 3 | diagonal and equal | 3 | 292.69 |
| 6 | diagonal and unequal | 3 | 295.62 |
| 10 | unconstrained | 1 | 298.81 |
| 11 | unconstrained | 2 | 317.56 |
| 12 | unconstrained | 3 | 340.87 |

| *Illex coindetii* - Western Mediterranean | | | |
|---|---|---|---|
| MODEL | R | m | AICc |
| **1** | **diagonal and equal** | **1** | **-219.27** |
| 7 | equalvarcov | 1 | -219.22 |
| 4 | diagonal and unequal | 1 | -213.34 |
| 2 | diagonal and equal | 2 | -217.28 |
| 8 | equalvarcov | 2 | -217.07 |
| 5 | diagonal and unequal | 2 | -212.36 |
| 3 | diagonal and equal | 3 | -216.77 |
| 9 | equalvarcov | 3 | -216.72 |
| 6 | diagonal and unequal | 3 | -210.96 |
| 10 | unconstrained | 1 | -193.79 |
| 11 | unconstrained | 2 | -190.95 |
| 12 | unconstrained | 3 | -188.71 |

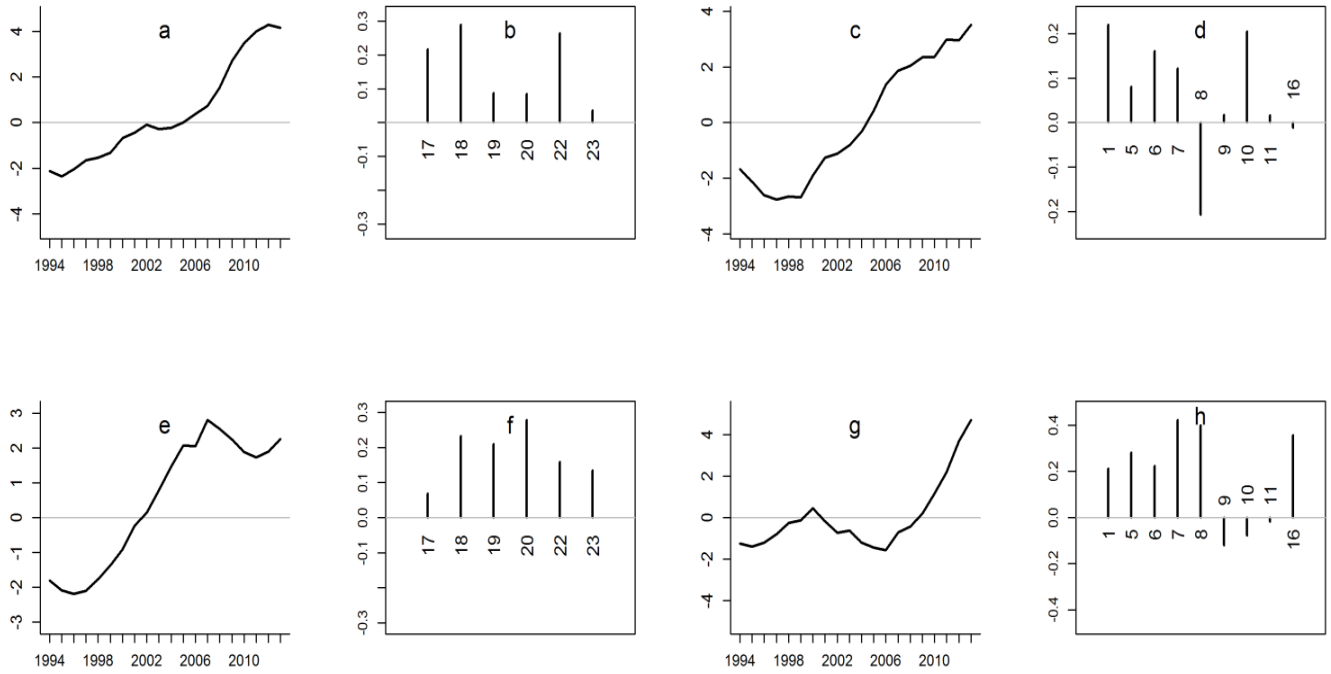



Figure 4.4: Common trends and factor loadings resulting from the Dynamic Factor Analysis of CPUE time series of *Octopus vulgaris* (above) and *Illex coindetii* (below) in the eastern (left) and western (right) basin during 1994-2013. GSAs are denoted by their numbers and located as seen in Figure 4.1. All y-axes are unitless.

### 4.4.4 General Linear Models

The best model predicting the non-standardized CPUEs of octopus was obtained including the factor GSA only (Table 4.2). In the standardized model, both Chla content of the spring concurrent with the surveys and the SST of the previous winter were retained in the best model (Fig 4.5 a + b). Both parameters negatively affected the inter-annual octopus abundances, independently of the region.

Table 4.2: Results of both non-standardized and standardized Generalized Linear Models for *Octopus vulgaris* and *Illex coindetii*. The five best models for each case are shown (best model in bold; significant variables marked by an asterisk for $p<0.05$ and by + for $p<0.1$). For each model, the covariates, the degrees of freedom (df), and the corrected Akaike Information Criterion (AICc) are given. Covariates: Year of sampling (factor, year), GSA (factor, gsa_f), mean chlorophyll a concentration in spring or winter (Chl_Spring, Chl_Winter, in $mg \cdot m^{-3}$) and mean SST in spring or winter (SST_Spring, SST_Winter, in ºC).

| Octopus non-standardized model | df | AICc | Octopus standardized model | df | AICc |
|---|---|---|---|---|---|
| **gsa_f** | 16 | 389.09 | **Chl_Spring * + SST_Winter$^{+}$** | 4 | 72.20 |
| gsa_f + Chl_Spring | 17 | 390.20 | Chl_Spring | 3 | 73.96 |
| gsa_f + Chl_Spring + SST_Winter | 18 | 391.27 | SSTSpring | 3 | 75.35 |
| gsa_f + year_f | 30 | 396.32 | Chl_Spring + SST_Spring | 4 | 75.65 |
| gsa_f + year_f +SST_Spring | 31 | 396.46 | Chl_Winter | 3 | 76.21 |

| Illex non-standardized model | df | AICc | Illex standardized model | df | AICc |
|---|---|---|---|---|---|
| **gsa_f + SSTSpring* + Chl_Winter$^{+}$** | 18 | 541.86 | **SST_Winter$^{+}$** | 3 | 64.54 |
| gsa_f + Chl_Winter | 17 | 542.70 | Chl_Winter + SST_Spring | 4 | 65.00 |
| gsa_f | 16 | 544.15 | Chl_Winter + SST_Winter | 4 | 65.32 |
| gsa_f + SST_Winter + Chl_Winter | 18 | 544.33 | SST_Spring | 3 | 65.47 |
| gsa_f + year_f + Chl_Winter | 31 | 547.00 | Chl_Winter | 3 | 65.87 |

The best fit for squid in the non-standardized model was obtained including the GSA as factor, the Chla content of the preceding winter and the SST during spring (Table 4.2). The coloured residuals evidenced that the negative effect of Chla on CPUEs was due to a geographic gradient in productivity (Fig 4.6 a). The SST had a slightly positive effect on squid CPUEs that was also due to the thermal geographic gradient in the Mediterranean (Fig 4.6 b). The model of standardized CPUEs revealed that the SST of the preceding winter positively affects inter-annual squid abundances, independently of the mean CPUE per area (Fig 4.6 c).

In general, both the standardized and non-standardized models gave consistent results (Table 4.2). While Chla correlated negatively with CPUEs, the correlation between CPUEs and SST varied with species and was negative for octopus, but positive for squid.

The factor GSA improved the un-standardized models only, while the factor year resulted to be non-significant.

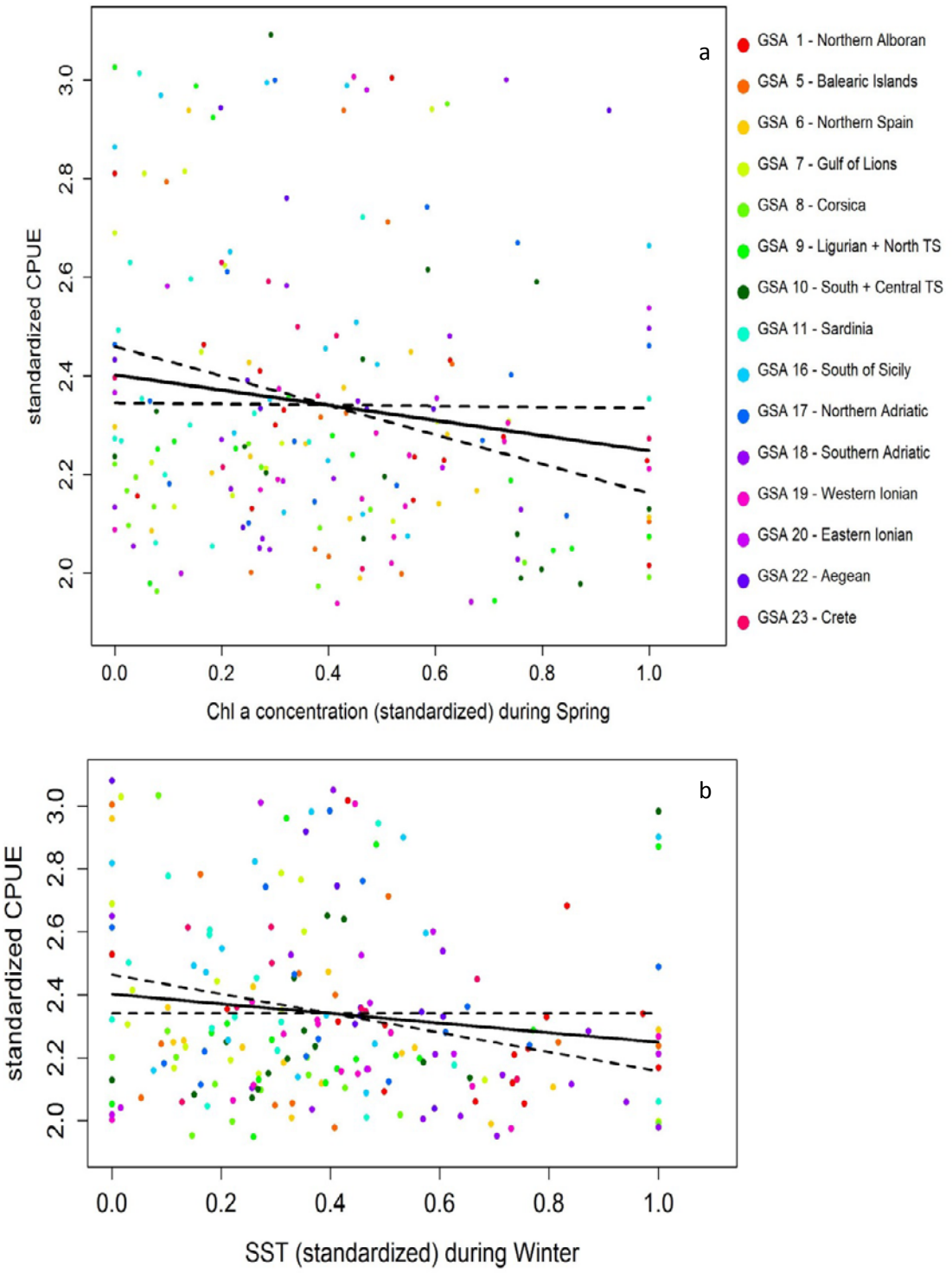



Figure 4.5: Model predictions and confidence intervals (dashed lines) of the effect of Chla content (a) and SST (b) on *Octopus vulgaris* CPUEs (GLM results of the standardized best model). Partial residuals colours are coded by GSA. TS = Tyrrhenian Sea.

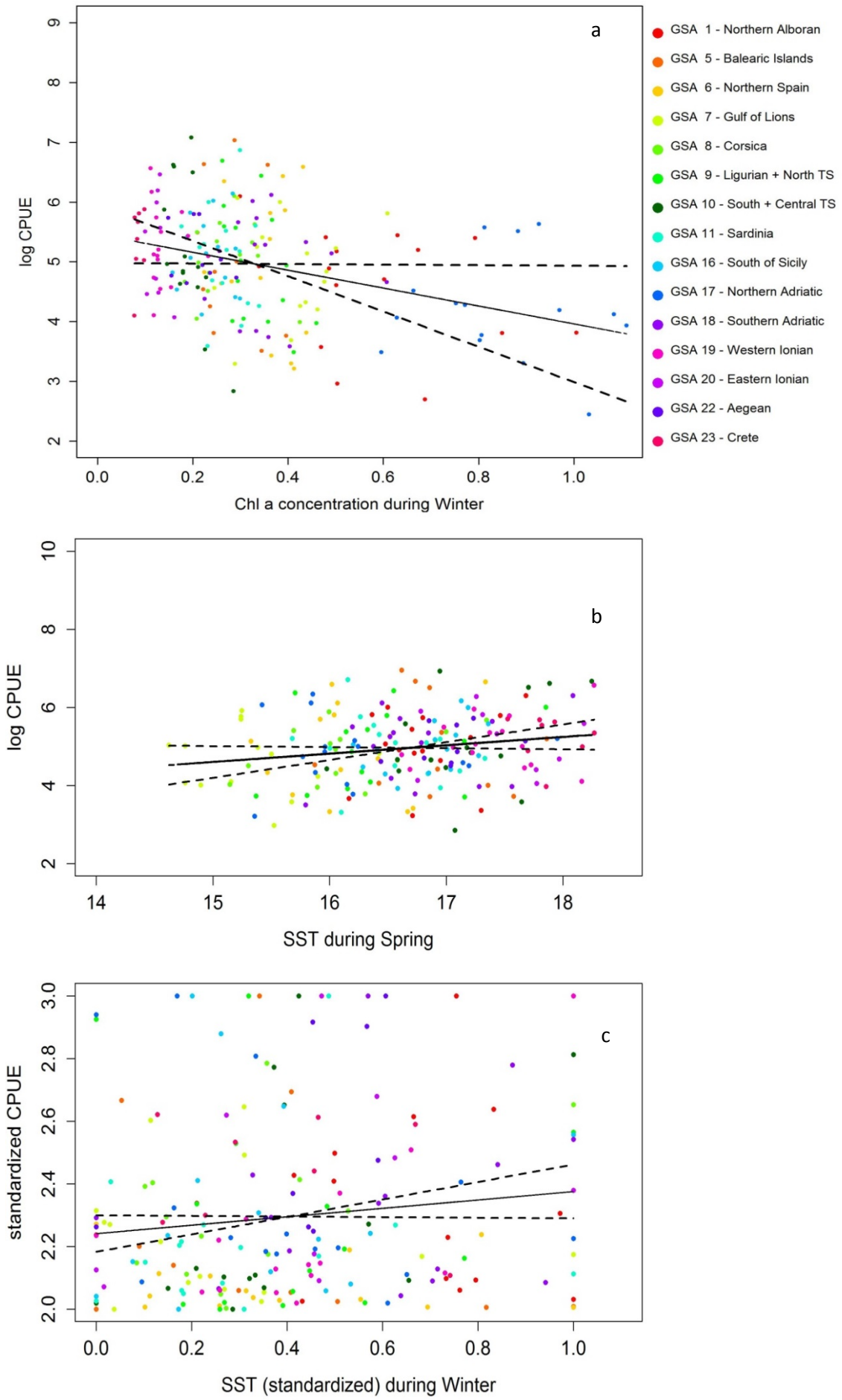
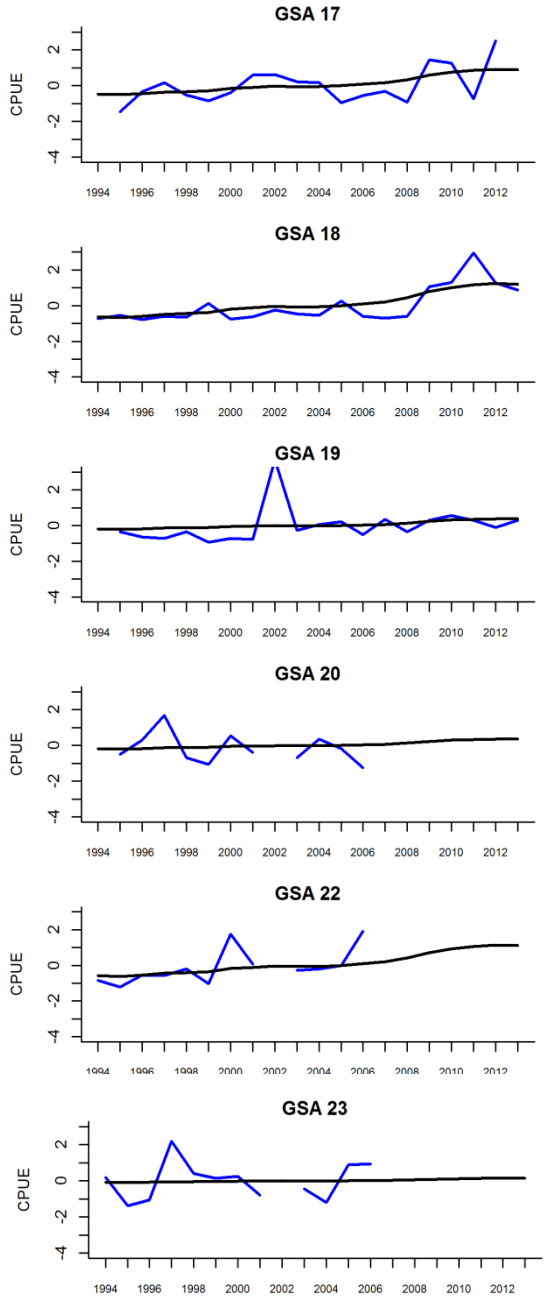



Figure 4.6: Model predictions and confidence intervals (dashed lines) of the effect of Chla content and SST on *Illex coindetii* CPUEs (GLM results): unstandardized (a+b) and standardized best model (c). Partial residuals colours are coded by GSA. TS = Tyrrhenian Sea.

Eastern basin




Western basin

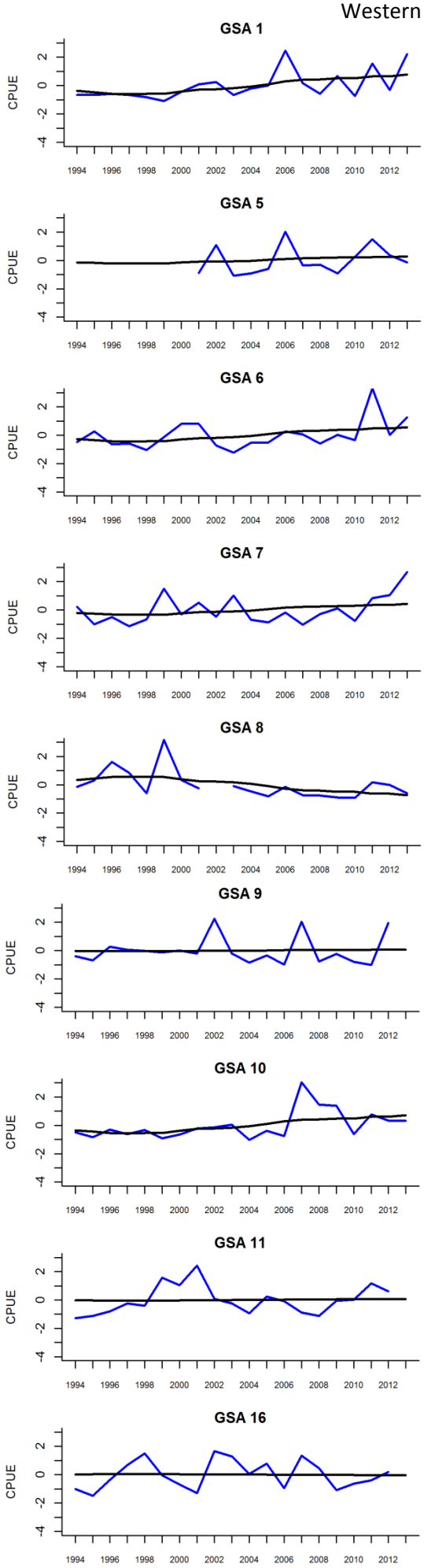



Figure 4.7: Model fits (blue lines) of the best models obtained by DFA on standardized CPUE time series for *Octopus vulgaris;* GSAs are separated into eastern (left) and western (right) basin.

Eastern basin

Western basin

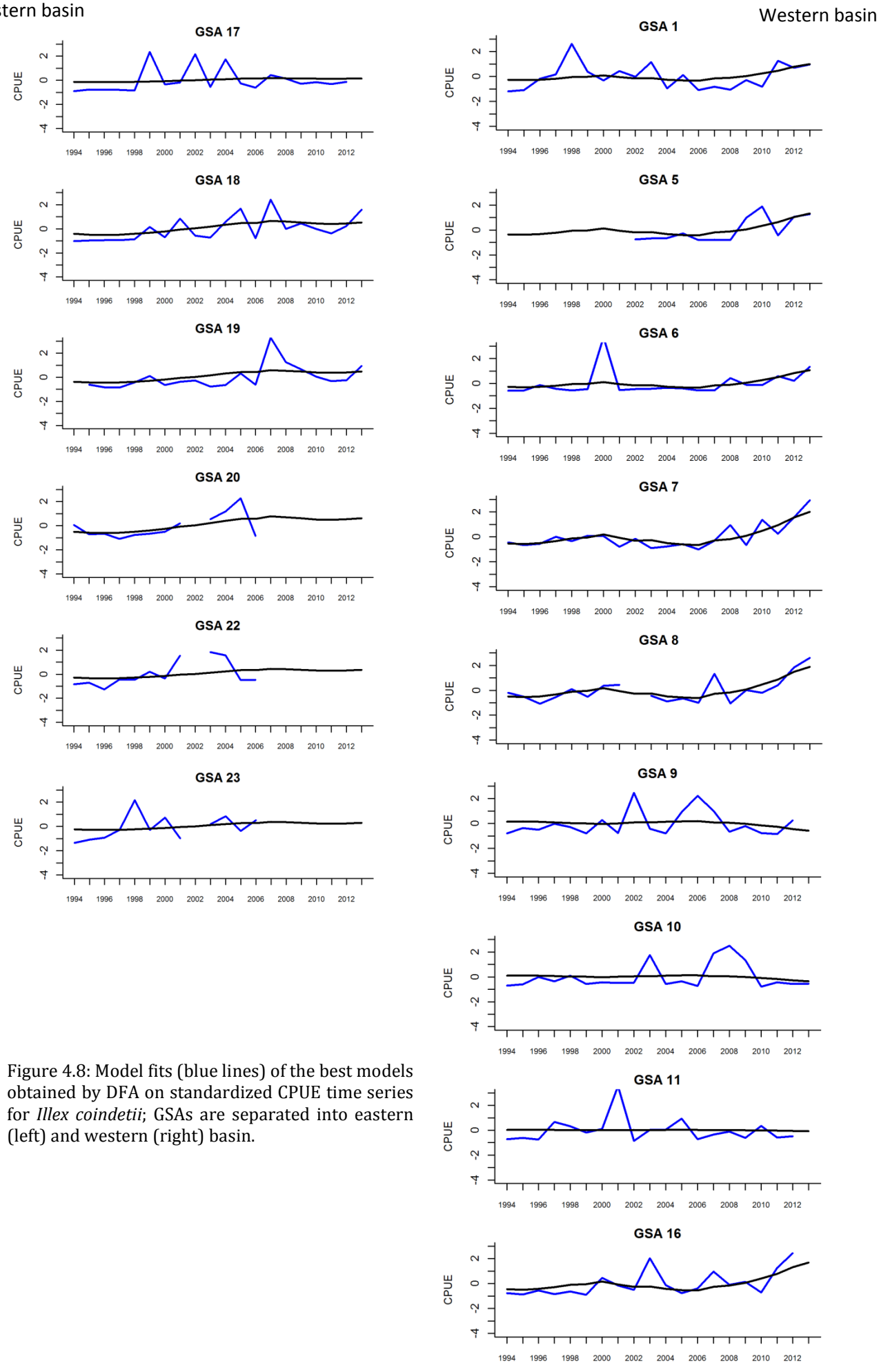



Figure 4.8: Model fits (blue lines) of the best models obtained by DFA on standardized CPUE time series for *Illex coindetii*; GSAs are separated into eastern (left) and western (right) basin.

## 4.5 Discussion

The strength and nature of the synchrony among populations affects the abundances, resilience and recovery of connected populations, with important implications for their management. In this study, large-scale population dynamics of two cephalopod species with contrasting life histories were analyzed combining three different methods. In the decorrelation analysis, higher correlation coefficients mean higher connectivity and therefore higher synchrony between locations. Similar dynamics have been revealed within smaller distances for octopus (*Octopus vulgaris*) than for squid *(Illex coindetii).* Our results are in accordance with a previous work at smaller spatial scale, where the correlation scale of *I. coindetii* was bigger than that of *O. vulgaris* both around the Balearic Islands and off the Mediterranean coast of the Iberian Peninsula (Puerta et al., 2016b). Results are likely related to the fact that *I. coindetii* is an oceanic species with higher mobility and a wider home range (Roper et al., 2010). This characteristic should lead to closer connections even between more distant populations of the squid. This neritic species also lives in deeper waters in the Mediterranean (Roper et al., 2010) and, therefore, most likely experiences a more homogeneous environment than the shallow-water octopus. Although it could be speculated that due to the squid's higher mobility, there are only 1-2 population in the Mediterranean, results of a recent research project reveal that, most likely, there are 4-8 separate stock units throughout this sea (Fiorentino et al., 2014). In contrast, for *O. vulgaris*, 3 (sub-)populations are considered most probable according to the project's report (Fiorentino et al., 2014).

The DFA results revealed that populations of both species followed the modelled common trends in all (eastern basin) or most (western basin) study areas. Synchronic population fluctuations can be due to different mechanisms such as (Liebhold et al., 2004; Gouhier et al., 2010): i) predator-prey interaction; ii) dispersal of individuals between populations; or iii) large-scale climatic events or environmental influences affecting various populations in the same way. The first one is very improbable due to the nature of cephalopods as rather unselective and adaptable predators (Rodhouse and Nigmatullin, 1996; Coll et al., 2013) and the different interannual prey dynamics in such a heterogeneous system as the Mediterranean. Connectivity via dispersal should lead to more similar abundance time series in neighbouring areas, but our results of the decorrelation analysis do not support a direct linkage over many hundreds of kilometres either. Therefore, the observed abundance fluctuations are more likely due to large-scale climatic phenomena or synchronous environmental influences.

Supporting the last hypothesis, our results revealed a negative influence of chlorophyll *a* content (Chla) on the abundances of both cephalopod species, a result that has already been reported on a smaller scale in the Western Mediterranean for *I. coindetii* (Puerta et al., 2015). Those authors argue that small pelagic fishes, which make up an important part of the Mediterranean food chain (Coll et al., 2006), are effective competitors for food with early and juvenile stages of squid species like *I. coindetii*. Higher Chla contents will usually foster the survival and growth of small fish, enhancing food competition and, thus, reduce cephalopod survival and abundance. The mechanism does not seem to differ among different areas, as interactions between Chl / SST and GSA were not significant. The

GSA was only statistically significant in the non-standardized models, accounting for abundance variability among areas.

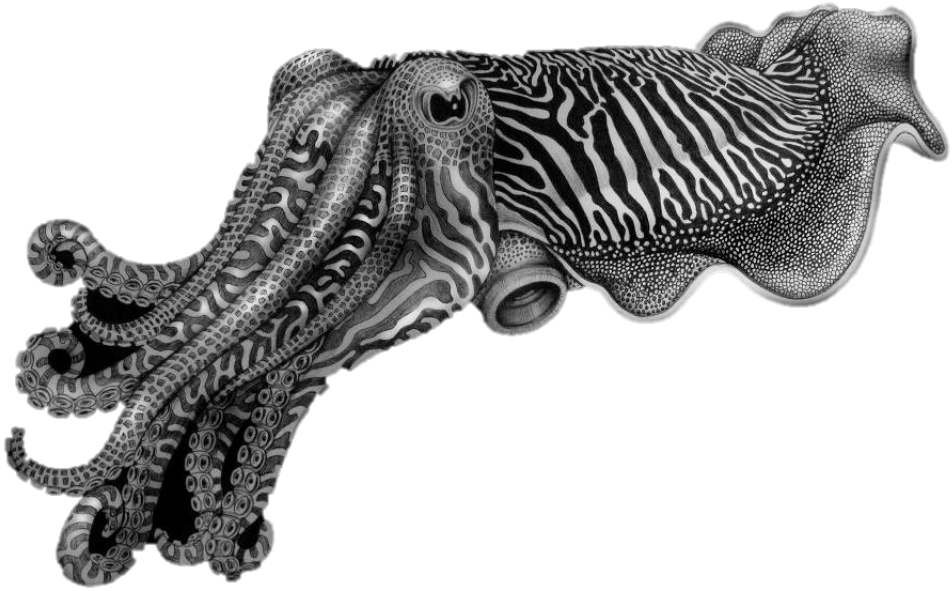
Apart from productivity, rising temperatures would cause declining abundances in octopus (standardized model), but warmer areas do not necessarily have fewer octopus, as other factors apparently play a more crucial role in determining their abundances and distribution. The mechanism for the negative temperature effect could be a stronger and more durable stratification of water masses during summer, causing less nutrient mixing and therefore lower phytoplankton and zooplankton growth rates. Warmer temperatures indeed induced a reduction of zooplankton abundance together with a change in community composition and structure in the study area (Fernández de Puelles et al., 2008), which might negatively affect zooplankton consumers. The common octopus preys directly on zooplankton during its paralarval stage (Roura et al., 2010) but it is also indirectly linked to zooplankton abundance via the food web, as it mainly consumes small mollusks and crustaceans (Quetglas et al., 1998; Roura et al., 2010). For squid, the temperature effect is different, as warmer areas show higher abundances (non-standardized model) and SST positively influences inter-annual abundance changes (standardized model). Warmer ecosystems support higher metabolic rates, higher food intake and growth (Segawa and Nomoto, 2002; Semmens et al., 2004) and can therefore foster higher squid abundances.

Our study reveals, for the first time, increasing trends in population abundance of two cephalopod species throughout the entire Mediterranean over the last 20 years, which is in accordance with the worldwide global trend reported recently (Doubleday et al., 2016). While the GLM results show the importance of Chla and SST on the abundance of both species, the similar trends in all the 15 survey areas of very different temperature and productivity regimes suggests that additional forces, acting at regional scale, are at play. The rising abundances are likely to be due to the constant, high fishing effort in this sea over decades (Colloca et al., 2013; Vasilakopoulos et al., 2014), reducing (directly or indirectly) the abundance of key cephalopod competitors and predators like bony fish, sharks and whales. Various studies have already observed changes in food webs, where the missing predators have been replaced by lower-level species (Pauly et al., 1998; Myers and Worm, 2003; Frank et al., 2005). While depletion of their predators releases the predation pressure on cephalopods (Caddy and Rodhouse, 1998), (over)fishing of species with similar habitat and resource needs will release competition pressure and open new ecological niches. Cephalopods are fast-growing, opportunistic and adaptable species with short generation times. They are generalist predators, which enables them to take advantage of changing trophic relations and rapid colonisation of new habitats (Jackson and O'Dor, 2001; Rodhouse et al., 2014). Therefore, ecosystem changes due to fishing exploitation could explain some of the observed rising catches of cephalopod species around the world (Caddy and Rodhouse, 1998; Vecchione et al., 2009), even though opinions differ on the importance and implication of other factors such as changed fishing tactics, new techniques and gears, license issues and environmental influences (Balguerías, 2000). While the direct impact of the commercial fishery on stocks is evident, amount and composition of bycatch may play an indirect role by supplying additional food to scavengers like crustaceans, an important prey of octopus species (Oro et al., 2013). Crustaceans often survived being discarded, and the commercial fishery may therefore indirectly cause an increase in octopus abundances in two different ways (Balguerías, 2000).

Climate change, or the synchronic effects of climate and harvesting, might also explain the proliferation of cephalopods (Doubleday et al., 2016). Apart from the discussed effect of rising temperatures, it causes further ecosystem changes (e.g. acidification, distribution shifts, altered productivity regimes, enhanced stratification) which may lead to competitive advantages for this taxon (Hoving et al., 2013). However, on a physiological and morphological basis, the effects of climate change will likely be negative at least at the early life stage, leading to a complex response of still uncertain direction (Pecl and Jackson, 2008). In terms of primary production, the two Mediterranean basins are likely to be affected by climate change in different ways (Macias et al., 2015): while the eastern basin will probably experience an increase in Chla due to vertical density changes caused by a combination of warming and salinization, the western basin is expected to have decreasing Chla concentrations. According to our results this would lead to increasing cephalopod abundances in this basin, while their abundance would decrease in the eastern basin. However, it is still a matter of further research whether other influences and ecosystem changes will mask and buffer this effect.

On smaller spatial scales, additional oceanographic features can cause synchronic population dynamics. Specific local conditions may explain the rather stable squid abundance (Fig 4.8) in the Tyrrhenian and Ligurian waters (including all waters around Sardinia), where eddies might retain paralarvae, causing a separate population dynamic in these waters. In the Ligurian Sea, this mechanism of retention has already been proposed to be of relevance for hake larvae (Abella et al., 2008). Furthermore, these waters are characterised by resident Atlantic waters, which are more saline than Spanish and French coastal and off-shore waters (Reglero et al., 2012). Other local scale processes leading to separate population dynamics are river run-offs, which have been suggested to foster the abundances of certain cephalopod species including *O. vulgaris* and *I. coindetii* (Lloret et al., 2001; Puerta et al., 2014, 2016b).

Up to now, all available studies investigating the influence of environmental and climatic effects on cephalopod populations from the Mediterranean Sea were carried out at local scales (Lloret et al., 2001; Quetglas et al., 2013; Keller et al., 2014 / Chapter 5; Puerta et al., 2014, 2016b). However, analysis at broader spatial scales are needed, especially in the framework of the regionalisation process envisaged under the new CFP (Article 18 of the EU Regulation Nº 1380/2013). In this sense, our study, which encompassed the whole Mediterranean basin, constitutes an important step forward with clear relevance for fisheries management in the area. Our results and those from previous works seem to be at odds with the regionalisation objectives. Cephalopods from the western basin, even those of high mobility rates like squids, displayed complex population structures and dynamics at local scales (Puerta et al., 2014) and were correlated only within a radius of a few hundred kilometres (Puerta et al., 2016b; this work). Nevertheless, the situation may differ between basins because populations from the eastern basin were more strongly connected than those from the western basin. In spite of the population complexities, our work also revealed common trends of rising abundances during the last 20 years, which agree with the global proliferation of cephalopods (Doubleday et al., 2016).



# Chapter 5

# Influence of environmental parameters on the life-history and population dynamics of cuttlefish *Sepia officinalis* in the western Mediterranean

# Chapter 5

# Influence of environmental parameters on the life-history and population dynamics of cuttlefish *Sepia officinalis* in the western Mediterranean

## 5.1 Abstract

The cuttlefish *Sepia officinalis* constitutes an important fishery resource in the Mediterranean, where it is exploited by both the bottom trawl and small-scale fleet. However, there is currently scarce information on the Mediterranean stocks, since most studies on the population dynamics of this species have been undertaken in the northeast Atlantic. In this work we first analysed different aspects of the cuttlefish life-history from the western Mediterranean such as population structure, reproduction and the trade-offs between somatic condition and reproduction investments. Secondly, we investigated the effects of different environmental parameters (e.g. climate indices, sea surface temperature (SST), rainfall, chlorophyll *a* concentration (Chla) and moon phase) on these populations, analysing several landing time series spanning the last 45 years. Our results revealed that Mediterranean cuttlefish populations exhibit strong seasonal variations owing to a reproductive migration towards coastal waters. The positive relationships between somatic and reproductive condition pointed to an income breeder strategy; this was reinforced by the percentage of empty stomachs, which was lowest just before the reproductive period peak. Despite the putative high sensitivity of cephalopod populations to external abiotic factors, our results showed that Mediterranean cuttlefish populations were not affected by most of the environmental parameters investigated. Significant effects were found for SST and a local climatic index, but no or very weak influences were evident for other parameters such as large-scale climatic phenomena (e.g. North Atlantic Oscillation, Mediterranean Oscillation) or other locally-related variables (e.g. rainfall, Chla). Our results revealed a shift in the cuttlefish population dynamics in the early 1980s, which could be related to important changes in the local hydroclimatology reported by previous authors.

## 5.2 Introduction

Cephalopods play a pivotal role in marine food webs, both as voracious consumers and major prey of many predators, spanning from fishes to whales (Piatkowski et al., 2001; Rosas-Luis et al., 2008). Many cephalopod species are also important living marine resources, supporting relevant fisheries around the world (FAO, 2012). Therefore, fluctuations in cephalopod abundances due to natural (climate) or anthropogenic (harvesting) perturbations have significant implications for both commercial landings and marine ecosystems through both direct or indirect effects on different trophic levels (Pecl and Jackson, 2008; Andre et al., 2010). The impacts of such perturbations are furthermore aggravated by the high sensitivity of cephalopods to environmental conditions. Indeed, most cephalopod species are characterized by high growth rates and short life cycles (1-2 years), making their population sizes very dependent on the success of spawning and recruitment (Boyle and Rodhouse, 2005). Whereas juveniles and adults are primarily

affected by fishing exploitation, early life stages (paralarvae and recruits) are strongly influenced by environmental factors such as oceanic currents, temperature or food availability (Waluda et al., 1999; Dawe et al., 2000). According to recent reviews (Semmens et al., 2007; Pierce et al., 2008), the most investigated factors influencing cephalopod abundance and distribution include global climatic phenomena, temperature, productivity and rainfall. Large-scale climatic indices such as the North Atlantic Oscillation (NAO) have been shown to affect cephalopod populations from the European Seas (Sims et al., 2001; Pierce and Boyle, 2003; Otero et al., 2005). On the other hand, the effects of the global-scale index El Niño Southern Oscillation (ENSO) have been detected not only in the southeast Pacific waters where this phenomenon occurs (Waluda et al., 2004) but also in areas far away from its action centre (Quetglas et al., 2013). The availability of remotely-sensed ocean data during the last decade facilitated investigating the effects of some surface parameters on cephalopods, most notably sea surface temperature and surface primary production (Arvanitidis et al., 2002; Georgakarakos et al., 2002; Wang et al., 2003). Other works have focused on local weather-related variables such as rainfall, winds or river discharges (Lloret et al., 2001; Sobrino et al., 2002). Finally, a few studies have analyzed the influence of the moon cycle on some jigging squid fisheries (Chen et al., 2006; Cabanellas-Reboredo et al., 2012).

Since ancient times, the cuttlefish *Sepia officinalis* Linnaeus, 1758 has been an important living resource in the Mediterranean Sea, where fishermen take advantage of the seasonal movements of large individuals to coastal waters for mating and spawning (Mangold-Wirz, 1963; Boletzky, 1983). Despite the importance of cuttlefish as a fishery resource, only a study of Belcari et al. (2002) analyzes the exploitation patterns of the species in the western, central and eastern Mediterranean in detail. Concerning the western basin, existing multi-species fishery studies containing information on *Sepia* include a preliminary bioeconomic analysis of a trammel net fishery (Merino et al*.,* 2008) and a study on the harvesting and climate effects on the inter-annual variability of population abundances (Quetglas et al*.,* 2013). Regarding the ecology and population dynamics of cuttlefish, most works have been conducted in the northeast Atlantic, the majority of them in waters of the Bay of Biscay and the English Channel (e.g. Denis and Robin, 2001; Wang et al*.,* 2003; Royer et al*.,* 2006), but also off the Portuguese coast (Fonseca et al*.,* 2008). Although there are many results from laboratory studies (Clarke et al., 1989; Forsythe *et al*., 1994, Boletzky and Hanlon, 1983; Boletzky, 1987), few studies have been undertaken in the Mediterranean. Apart from the comprehensive work of Mangold-Wirz (1963), there is a study on the reproductive biology of *Sepia* from the Aegean Sea (Önsoy and Salman, 2005) and a fecundity study by (Laptikhovsky et al., 2003).

In the Balearic Islands (western Mediterranean), cuttlefish is exploited by both the bottom trawl and the small-scale fleet. While bottom trawlers capture the species as a by-catch on continental shelf grounds deeper than 50 m all year round (Quetglas et al*.,* 2000), cuttlefish supports an important seasonal small-scale trammel net fishery taking place in coastal waters (Merino et al*.,* 2008). The main objective of this work was to analyze both intra-annual and inter-annual population dynamics of cuttlefish in the western Mediterranean. With this aim, we first analyzed different aspects of the cuttlefish life-history (population structure, reproduction and the trade-offs between somatic condition and investment in reproduction) influencing the intra-annual population dynamics in the study area. In addition, we investigated the effects of different environmental parameters

(e.g. climate indices, sea surface temperature, rainfall and moon phase) on the seasonal and inter-annual variation of the population abundance, analysing time series of landings embracing the last 45 years to shed new light on the natural drivers shaping the population dynamics of the species.

## 5.3 Material and methods

To investigate life-history related aspects, monthly biological sampling was carried out during the seasonal small-scale trammel net fishery (January-July) in two consecutive years (2007, 2008). Additionally, biological samples from annual spring (June) scientific trawl surveys (2004-2011) were included in the calculation of the length weight relationship. To obtain monthly size distributions for the trawl fraction, we performed monthly size frequency sampling aboard commercial bottom trawlers between 2000 and 2011. A total of 949 (505 males, 444 females) and 2247 individuals were analyzed in the biological and size sampling, respectively. During the biological sampling, the following measurements were taken: sex, mantle length (ML, to the nearest mm), total and eviscerated weight (TW and EW, respectively, both to the nearest 0.1 g), gonad weight (GW), digestive gland weight (DGW) and stomach weight (all to the nearest 0.01 g).

To determine the relationship between ML and TW, the parameters of the power formula $TW=a(ML)^b$ were calculated for females, males and for the total. The slopes and the intercepts were compared between sexes applying an analysis of covariance (ANCOVA) to the log-transformed linear relationships. The size-frequency distributions of the small-scale and the bottom trawl fractions were obtained in order to compare their size structure. To determine intra-annual differences in the proportion of males and females in the population, the sex-ratio was analyzed monthly and differences were tested by using the Chi-square test. Sexual development was determined through the monthly evolution of the gonadosomatic index ($GSI=100 \cdot GW/(TW-GW)$). To infer relationships between reproduction and food intake, the monthly evolution of both the digestive gland index ($DGI=100 \cdot DGW/(TW-DGW)$) and the percentage of empty stomachs (emptiness index, EMI) were computed.

For the investigation of individual body condition and the relationship between somatic and reproductive investment, reduced major axis regression (RMA; Bohonak and van der Linde, 2004) was used. This regression technique was developed for cases where the independent variable is measured with error, because in such a case the slope estimation calculated using ordinary least square regression methods is biased (Sokal and Rohlf, 1995). After regression equations were calculated for log-transformed ML-EW and ML-GW relationships, residuals were obtained and standardized by dividing each by the standard deviation of the predicted values. These residuals provide a size-independent measure for comparing the relative condition of somatic and gonad tissues, considering that individuals with heavier tissues for their length (higher residuals) are in better condition (Hayes and Shonkwiler, 2001). Hence, ML-EW and ML-GW residuals were used as indicators of somatic condition (SC) and reproductive condition (RC) respectively. To determine trade-offs in energy allocation, SC was modeled against the explanatory variables month, size (ML) and RC. Although data were size-corrected for linear effects, ML was still included in

the model to analyze its non-linear effect. As multiple variables were analyzed and non-linear relationships were expected, generalized additive models (GAMs) were applied.

In order to investigate the effects of environmental conditions on cuttlefish populations, two time series of landings at different temporal scales were analyzed: 1) monthly total landings (pooled bottom trawl and small-scale) from 1965 to 2011; and 2) daily catches per vessel between 2000 and 2011. All cuttlefish landing data were supplied by the fish auction wharf of Mallorca. Landings were used as a proxy of abundance owing to the fact that: 1) discards are negligible; 2) landings and CPUE's are highly correlated (see Quetglas et al. 2013); and 3) landings and effort are not correlated (see Pierce *et al*, 1994) (Fig 5.1).

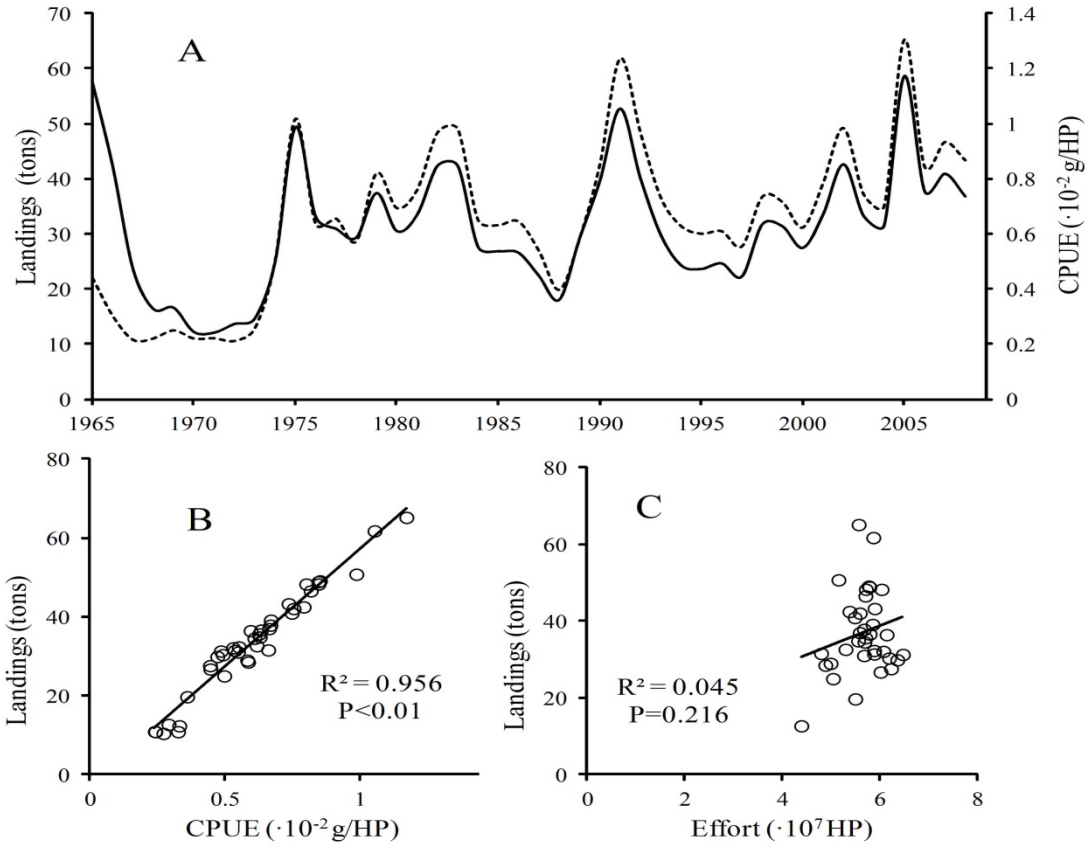



Figure 5.1: Time series of cuttlefish (*Sepia officinalis*) landings (continuous line) and catch per unit effort (CPUE; dotted line) from the Balearic Islands (western Mediterranean) during 1965-2009 (A); relationships of cuttlefish landings against CPUE (B) and fishing effort (C) with the corresponding linear fit.

We modelled the effects of climatic indices at different spatial scales together with several local environmental parameters on cuttlefish landings. The large-scale North Atlantic Oscillation (NAO) measures the difference in the normalized sea-level pressure between the Azores and Iceland (Hurrell, 1995) and influences the climate variability in the Mediterranean Sea. Two Mediterranean climate indices were also used: the Mediterranean

Oscillation Index (MOI), which indicates the normalized pressure difference between Gibraltar's Northern Frontier and Lod Airport in Israel (Palutikof, 2003), and the Western Mediterranean Oscillation index (WeMO) representing pressure differences between Padua in Italy and Cádiz in Spain (Martin-Vide and Lopez-Bustins, 2006). At a smaller spatial scale, a local climatic index (LCI) already used in the study area (Fernández de Puelles and Molinero, 2007; Hidalgo et al., 2011) was analyzed. This index quantifies the regional hydroclimatic variability around the Balearic Islands synthesizing the following variables by means of the first axis of a PCA (for details, see Molinero et al., 2005): monthly anomaly fields of surface air temperature, sea surface temperature, atmospheric sea level pressure, 500 hPa geopotential height and precipitation records (Kalnay et al., 1996). High LCI values are associated with higher temperatures, drier conditions and weaker winds compared to low LCI values.

The local environmental variables analyzed included the monthly mean sea surface temperature (SST), which was obtained from two sources: a) modelled SST data from 1965 until today (SSTa); and b) satellite-derived data from 2000 to 2009 for the area where the main fishery of *Sepia* takes place (SSTb). Chlorophyll *a* concentration (Chla) was used as a proxy for food availability and was modelled using different time lags (1, 2 and 3 months) to account for the time required for energy transfers between trophic levels. Additionally, rainfall was data from the study area was included in the analysis. To avoid the seasonal pattern being reflected in the variables SST, Chla and Rainfall, anomaly data was used, calculated as the residuals obtained by modeling SST / Chla / Rainfall versus Month and Year. From now on we refer to these anomalies when mentioning these model parameters. Finally, the lunar cycle was accounted for. Moon phases were calculated as daily sin-transformed fraction of the moon illuminated (Kuparinen et al., 2010), with values oscillating between 1 (full moon) and -1 (new moon). The lunar cycle was treated as a factor of four levels accounting for lunar phases from new moon (1) to full moon (4). As the lunar influence might be more evident during the reproduction period when animals might be more sensitivity to external conditions (see Wingfield and Sapolsky, 2003), the interaction between lunar phase and season was modeled. In this case, and to simplify the interaction term, season was treated as a factor with two levels, first and second semester, accounting for the reproduction and non-reproduction periods, respectively. The variable year was included in the models to take into account density-related dynamics independent from the environmental processes. To test its influence, we first checked that results of models with and without year gave similar results. Secondly, year was modeled against each environmental parameter separately and in all cases it never explained more than 17.3% of the variance.

The effects of environmental parameters on cuttlefish landings were also analyzed with GAMs. Since the data available covered different time series and temporal scales, three models were fitted. These three models, together with the data sources of all environmental parameters, are shown in Table 5.1. After testing for colinearity of parameters by analyzing linear pairwise correlation coefficients and calculating the variance inflation factor (VIF), a stepwise approach was adopted to select the best model. First, non-significant variables were removed one by one unless their removal resulted in a higher Akaike information criterion (AIC). Afterwards, significant variables were excluded whenever their removal resulted in a better model fit according to the minimization of the generalized cross-validation criterion (GCV) and the AIC. The response variable (landings) and the

explanatory variable rainfall were log-transformed to obtain normalized distributions. All GAM analyses performed in this study were carried out with the R package (version 2.15.1; http://www.r-project.org/) using the mgcv library. For all GAMS, residuals were checked for homogeneity of variance, absence of temporal (inter-annual) autocorrelation and violation of normality assumptions.

Table 5.1: Main characteristics (time series, time scale, explanatory variables) of the three different models fitted in this study along with the sources of the datasets used. NAO: North Atlantic Oscillation; MOI: Mediterranean Oscillation Index; WeMO: Western Mediterranean Oscillation; $SST_a$ and $SST_b$: modeled and satellite-derived Sea Surface Temperature anomaly, respectively; LCI: Local Climate Index; Chla: chlorophyll *a* concentration anomaly.

| | Time series | Time scale | Explanatory variables |
|---|---|---|---|
| Model I | 1965-2009 | Monthly | Year, month, NAO[1], MOI[2], WeMO[3], LCI[4], rainfall[5], $SST_a$[4] |
| Model II | 2000-2009 | Monthly | Year, month, $SST_b$[6], Chla[6], rainfall[5] |
| Model III | 2000-2010 | Weekly | Year, semester, moon phase[7], rainfall[5] |

[1] http://www.cpc.ncep.noaa.gov/products/precip/CWlink/pna/nao_index.html
[2] http://www.cru.uea.ac.uk/cru/data/moi/
[3] http://www.ub.edu/gc/English/wemo.htm
[4] http://www.esrl.noaa.gov/psd/data/reanalysis/reanalysis.shtml
[5] http://www.aemet.es/es/web/serviciosclimaticos/datosclimatologicos/valoresclimatologicos
[6] http://gdata1.sci.gsfc.nasa.gov/daac-bin/G3/gui.cgi?instance_id=ocean_month
[7] http://aa.usno.navy.mil/data/docs/MoonFraction.php

## 5.4 Results

### 5.4.1 Life-history traits

The ANCOVA revealed significant differences ($p<0.001$) between sexes in the length-weight relationships (females: $a=3\cdot10^{-4}$, $b=2.812$, $R^2=0.983$; males: $a=5\cdot10^{-4}$, $b=2.695$, $R^2=0.982$). Males outnumbered females between February and April ($p<0.05$, $\chi^2$-test). Cuttlefish sizes from the small-scale fishery ranged from 8-24 cm ML and showed a main modal size at 10-11 cm ML and a minor mode at 19-20 cm ML, while individuals from the bottom trawl fishery ranged from 4-21 cm ML and showed a main modal size at 12-13 cm ML (Fig 5.2 A). In both fisheries, the landings displayed a clear seasonal trend (Fig 5.2 B), with small-scale landings peaking in March before plummeting down until August and remaining very low until December. By contrast, bottom trawl catches peaked in February and decreased down to July, increasing markedly afterwards. Mean monthly sizes showed the same pattern, increasing from January (~12.5 cm ML) to March (~14.5 cm ML) and decreasing until July (~10.5 cm ML) in the small-scale fishery (Fig 5.2 C). Individuals from the bottom trawl fleet decreased from mean sizes of 13.5 cm ML during January down to 10.5 cm ML in August, increasing progressively up to 11.5-12.5 cm ML in October-December (Fig 5.2 D).

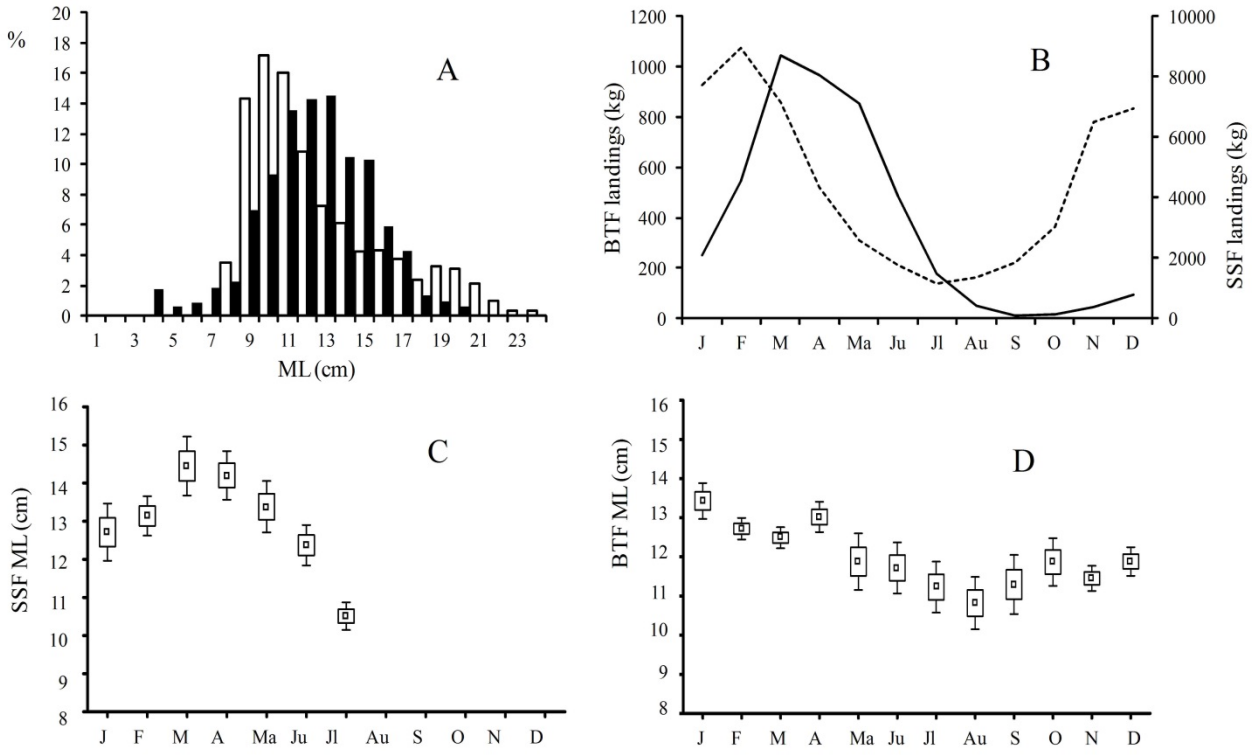



Figure 5.2: Cuttlefish (*Sepia officinalis*) populations caught by the bottom trawl (BTF) and small-scale (SSF) fleets from the Balearic Islands (western Mediterranean) during 2000-2011: A) Total size-frequency distributions (SSF: white; BTF: black); B) monthly landings (SSF: continuous line; BTF: dotted line); and mean sizes ± SD and the 95% CI (whiskers). of the SSF (C) and BTF (D). BTF and SSF distributions were obtained using individuals taken during January-December and January-July, respectively.

The mean gonadosomatic index (GSI) in females increased from January to March, remained at the highest values (~5%) between March and May, and decreased in June-July (Fig 5.3 A); in males, however, the GSI did not show important changes. Digestive gland index (DGI) values were always higher for females than for males. While the mean DGI decreased with time in males, such a decrease was only evident since April in females (Fig 5.3 B). Although in general the Emptiness Index (EMI) was higher in males than in females (Fig 5.3 C), the mean values showed a similar increasing trend from February to June in both sexes; it is noteworthy, however, that EMI values plummeted between January and February.

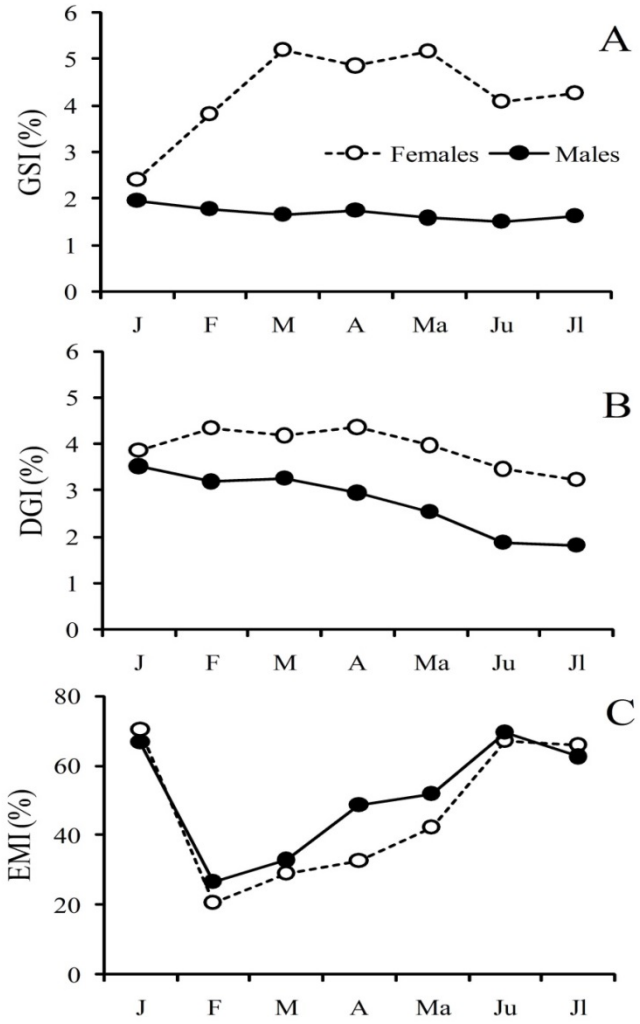



Figure 5.3: Monthly development of the gonadosomatic (GSI), digestive gland (DGI) and emptiness (EMI) indices of cuttlefish caught by the small-scale fleet from the Balearic Islands (western Mediterranean) during the fishing season (January to July), separated by sex.

The body condition analysis revealed important differences between sexes (Fig 5.4). The only common pattern was the increase of somatic condition (SC) with increasing reproductive condition (RC), although the relationship was markedly more linear and confident in males than in females. The temporal pattern of SC differed by sex: while the seasonal effect was most positive in January and became less positive with time in females, it was low in February and reached a maximum in May in males. In both sexes, the SC decreased with increasing size to about 15 cm ML, from where on it increased with increasing size.

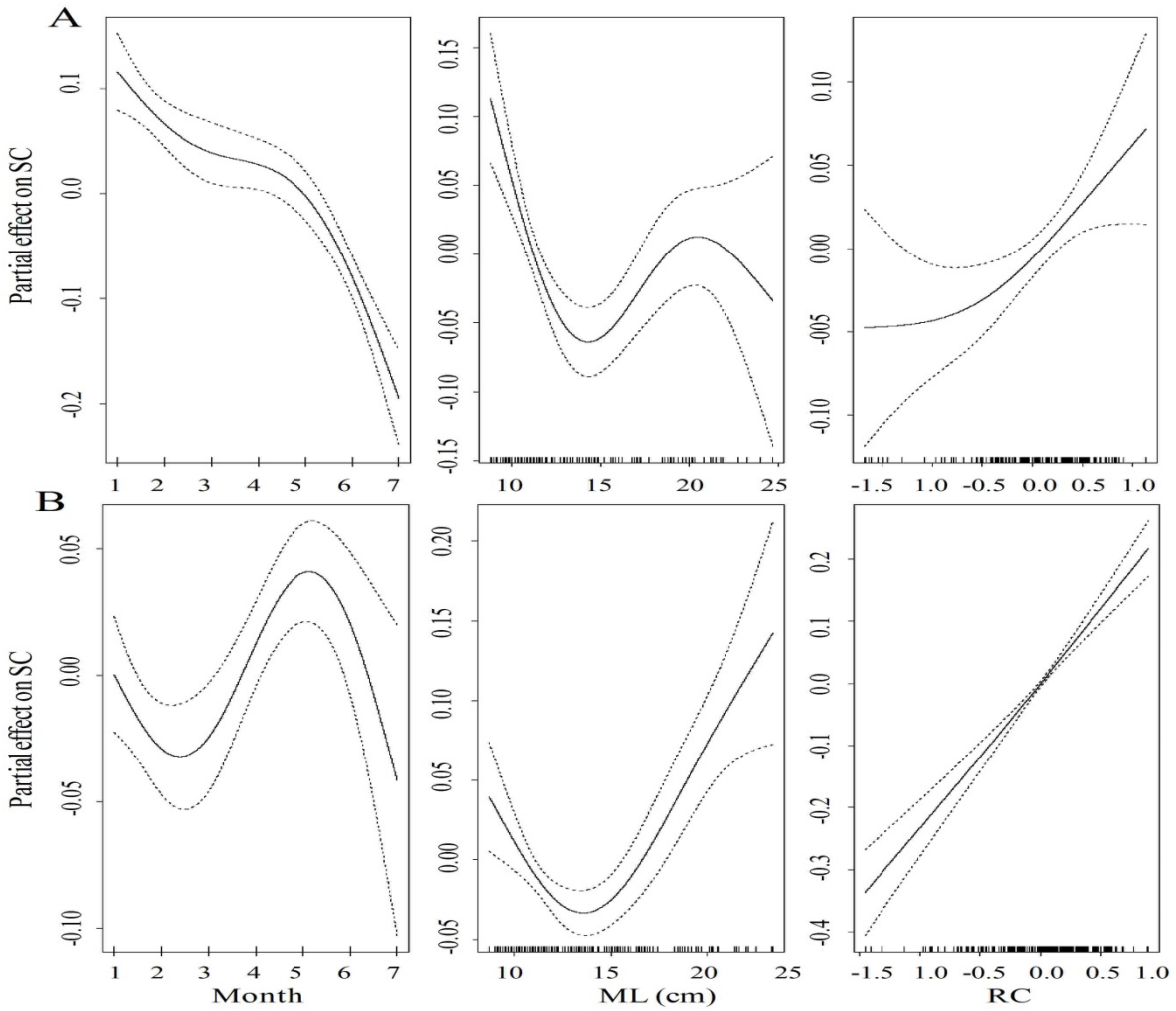



Figure 5.4: Generalized additive model (GAM) outputs showing the effects of month, size (ML) and reproductive condition (RC) on somatic condition (SC) of females (A) and males (B) cuttlefish from the Balearic Islands (western Mediterranean). Solid lines indicate the fitted partial effects, whereas broken lines are the 95% confidence intervals.

### 5.4.2 Environmental effects

Once the significant variables for each of the three models considered were selected, different GAMs were run to obtain the best fit based on the lowest GCV and AIC (Table 5.2).

Table 5.2: Selection of the best fit for each of the three models considered in this study (see Table 5.1). For comparative purposes, the two/three best fits are shown for each model. The final model (shown in bold) is the one having the lowest generalized cross validation (GCV) and Akaike information criteria (AIC) while explaining the same (or more) percentage of the deviance (%DE). LCI: local climatic index; $SST_a$ and $SST_b$: modeled and satellite-derived Sea Surface Temperature anomaly, respectively; MP: moon phase; SM: semester; N: sample size.

| | Response variable ~ Explanatory variables | %DE | N | GCV | AIC |
|---|---|---|---|---|---|
| Model I | Log Landings ~ s(Year, Month) +s(LCI) | **82.6** | **540** | **0.204** | **673.7** |
| | Log Landings ~ Year +s(Month) +s(LCI)+ s($SST_a$) | 73.9 | 540 | 0.321 | 914.8 |
| | Log Landings ~ s(Year) +s(Month) +s(LCI)+ s($SST_a$) | 67.1 | 540 | 0.373 | 1002.0 |
| Model II | Log Landings ~ Year +s( Month) + s(LCI) + s($SST_b$) | **94.1** | **117** | **0.109** | **71.61** |
| | Log Landings ~ s(Year) + s(Month) + s(LCI) + s($SST_b$) | 93.1 | 117 | 0.122 | 86.40 |
| Model III | Log Landings ~ Year + SM + s(log(rain + 1)) | **51,7** | **2752** | **0.916** | **7570** |
| | Log Landings ~ Year + SM + MP + s(log(rain + 1)) | 51.7 | 2752 | 0.917 | 7573 |
| | Log Landings ~ Year + s(log(rain + 1)) + MP + SM + MPxSM | 51.7 | 2752 | 0.919 | 7578 |

When analyzing model I (monthly data from 1965 to 2009), we did not find significant effects of either large scale climatic index (NAO, MOI or WeMO), the SST or the rainfall, and the final trials included year, month and LCI; the best fit was obtained combining the effects of year and month by means of a bivariate smoother. Landings increased with increasing LCI (Fig 5.5 A). The bivariate smoother revealed the appearance of a clear periodicity of about 10 years since the early 1980s characterized by an alternating seasonal dynamics (Fig 5.5 B). During periods of high abundance, the seasonal cycle is mainly dependent on the very high catches in spring with values close to the season's average in autumn. By contrast, during periods of low abundance, spring values are close to the season's average with very low catches in autumn shaping the seasonal pattern.

The final model II (monthly data from 2000 to 2009) included year as a factor and month, LCI and $SST_b$ as covariates, since the effects of Chla and rainfall were not significant. The model displayed an increasing trend in landings from 2000 to 2005 followed by a progressive decrease afterwards (Fig 5.5 C). The effect of month (Fig 5.5 D) depicted the strong intra-annual cycle with maximum values in spring and minimum values in autumn as already shown in Figure 5.2 B and the SST anomaly was positively correlated with landings. The partial linear effect of LCI is not shown because it resulted in a very similar graph to the one shown for model I.

Model III (weekly data from 2000 to 2010) revealed that the best model included year as factor, rainfall and semester. Rainfall displayed a negative and nonlinear effect with very light rainfall triggering a negative influence on the cuttlefish landings (Fig 5.5 F). The effect of year is not depicted because it is similar to that shown for model II; the factor semester is not shown as it provides the same information as the effect of month in model II. No significant interaction was found between semester and lunar cycle. Although

landings differed slightly during new and full moon compared to the second moon phase (Fig 5.5G), the effect was very weak and moon phase was therefore not included in the final model.

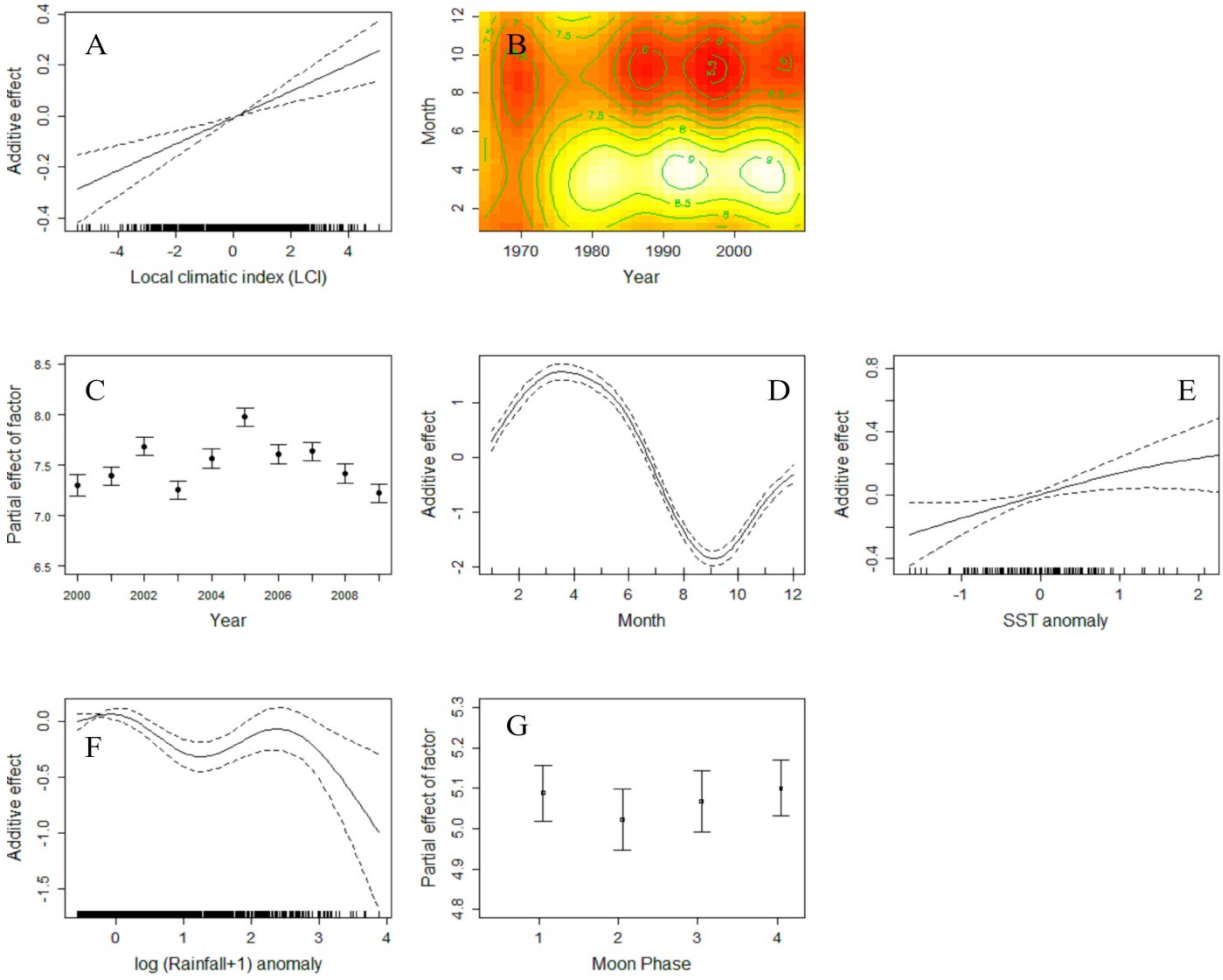



Figure 5.5: Outputs of the three generalized additive models (GAMs) fitted in this study (see Table 5.2). Graphs show the partial additive effects of different explanatory variables on cuttlefish landings (in log scale) from the Balearic Islands (western Mediterranean). The explanatory variables modeled are: A) Local Climatic Index (LCI); B) bivariate effect of year and month; C) year; D) month; E) SST anomaly; F) log (rainfall+1) anomaly; and G) moon phase, from new moon (1) to full moon (4). Although depicted here, the effect of the moon phase was very weak and therefore not included in the final model. In figure B, deep red colors represent the lowest influence on the response variable, lighter colors represent higher influence. For the continuous effect (LCI, month, SST anomaly, rainfall anomaly), solid lines indicate the fitted partial effects and broken lines the 95% confidence intervals (CI). For factors (year, moon phase), the mean ± the Standard Error are given. To avoid repetition, partial effects of year and LCI are only plotted once, although they occur in different models.

## 5.5 Discussion

Our study shows how the life-history dynamics of cuttlefish in the western Mediterranean is phenologically adapted to cope with the seasonal environmental variability that is ultimately reflected in their landings. As a result of its fast growth rate and short lifespan, cephalopods display a wide capacity for life-history and population plasticity

(Pecl and Jackson, 2008). In spite of this, there are currently few studies analyzing the effect of environmental conditions on Mediterranean cephalopod populations (e.g. Lloret et al., 2001; Lefkaditou et al., 2008; Cabanellas-Reboredo et al., 2012; Quetglas et al., 2013). Such analyses are especially important in the Mediterranean, an area highly susceptible to the climate change (Parry 2000; Coma et al. 2009) and supporting intense fishing exploitation rates (Colloca et al., 2011), where synergistic effects between climate and anthropogenic uses will likely exacerbate climate-induced changes (Quetglas et al., 2013).

Owing to the physiological plasticity of cephalopods, differences in cuttlefish life-history traits are expected in populations from areas with contrasting oceanographic conditions, such as the northeast Atlantic and the Mediterranean. Indeed, northeast Atlantic populations have larger modal sizes (for the trawling and small-scale fisheries respectively: 17 and 23 cm ML, Dunn, 1999; 16 and 12 cm ML, Coelho and Martins, 1991) than Mediterranean populations (8-12 and 10-14 cm ML, Belcari et al., 2002; 13 and 10 cm ML, this study). Differences also arise for the sex-ratio, which favored males during January-April in our study, but was balanced in the eastern Mediterranean (Önsoy and Salman, 2005) or showed annual changes in the northeast Atlantic (Coelho and Martins, 1991). However, Dunn (1999) found that the sex-ratio was balanced in northeast Atlantic populations from the trawl fleet, but favored males in those from the small-scale fleet. Consequently, differences in the proportion of sexes depending on the exploited fishing grounds, as we found in our samples, could indicate lag times in the seasonal movements between males and females. Indeed, based on the fact that males outnumbered females in July, Mangold-Wirz (1963) concluded that females leave the coastal waters earlier than males. The main reproductive period does not show important differences between the Mediterranean (March-June, Önsoy and Salman, 2005; April-June, Mangold-Wirz, 1963; March-May, this study) and the Bay of Biscay (March-June, LeGoff and Daguzan, 1991), whereas it spanned from February to July in the English Channel (Dunn, 1999). In the Mediterranean, as well as in estuarine valleys on the northwestern Spanish Atlantic coast, winter spawning has also been observed (Mangold-Wirz, 1963; Guerra 2006).

The annual evolution of landings of both the trawl and small-scale fisheries from our results gives interesting insights into spatial movements between the coastal waters (small scale fleet) and the shelf grounds deeper than 50 m (trawl fleet). The landings showed a strong seasonality with peaks in February (trawl fishery) and March (artisanal fishery), followed by a gradual decrease; only in the trawl fishery, landings increased again from July on. The lag time between the trawl and small-scale landing peaks indicates that the bulk of the cuttlefish migration takes place in March, whereas the lack of small-scale catches from July on marks the end of the reproductive period. The landing peaks coincide with those found by previous studies undertaken both in the Mediterranean (Belcari et al., 2002) and the English Channel (Dunn, 1999). In the Catalan Sea, Mangold-Wirz (1963) reported a peak in June, whereas Lloret and Lleonart (2002) found a rather different pattern with catches showing low seasonality and peaking in winter (November-January). Tallying with previous studies (Mangold-Wirz, 1963; Önsoy and Salman, 2005), the increase of the population mean size up to March and the subsequent decrease reveal the arrival of large, mature individuals and their subsequent disappearance from the fishing grounds after mating. Recruitment would take place during late summer, as suggest the increase of both the monthly mean size and the landings from August on. Such timing is congruent with the growth rates and development times given by Richard (1971), who suggested a period

ranging from 4.5 to 7 months, depending on the water temperature, between egg laying and recruitment of 5 cm ML cuttlefishes. This points to a synchronization between external conditions and recruitment taking place when environmental conditions, such as food availability, are optimal for offspring growth, a crucial prerequisite for the persistence of populations in oligotrophic systems such as the Mediterranean Sea (Hidalgo et al., 2011; Quetglas et al., 2011).

Cephalopod investments in reproduction are very high, especially in females: whereas gonad weight can reach up to 20-30% of the female's body weight, the values for males rarely exceed 5% (Forsythe and Van Heukelem, 1987). Consequently, strong relationships between reproduction and body condition are expected (Gabr et al., 1999a; Quetglas et al, 2011). Body condition depends either on energy stores or current food intakes (capital and income breeders, respectively; Roff, 2002). In the first case, energy is directly obtained from mantle tissues which serve as storing sources. These trade-offs are usually evident in species storing energy reserves while immature, which they later use for gonad growth during the maturation process. In the second case, gonads develop directly from a food source, which is used for somatic growth before maturation but directed to the gonads afterwards. Both the capital breeding (Gabr et al., 1999b; Jackson et al., 2004) and income breeding (Gabr et al., 1999a; Pecl and Moltschaniwskyj, 2006; Quetglas et al., 2011) strategies have been reported in cephalopods. Although less frequent, these two strategies can also be combined (Laptikhovsky and Nigmatullin, 1993). The positive relationships between somatic and reproductive condition that we found in both sexes points to an income breeder strategy, since trade-offs between stored reserves in somatic and reproductive tissues are inferred from negative relationships (Roff, 2002). This conclusion is further supported by the percentage of empty stomachs, which was lowest (20-25%) in February, just before the reproductive period peak (March to May), but then increased to about 65% at the end of that period. The positive relationship between somatic and reproductive condition implies that cuttlefish in good condition typically possess better reproductive condition (Pecl and Moltschaniwskyj, 2006). In female cuttlefish, such positive relationship might be regulated through the reabsorption of oocytes (Laptikhovsky et al., 2003).

In line with the aforementioned differences between sexes in reproductive investments, we found contrasting effects of month and size on the somatic condition in males and females. Whereas the somatic condition in females was highest before the reproductive period and decreased steadily with time, it increased since February up to a marked peak in May and decreased afterwards in males. Such contrasting responses might be due to the much higher energy requirements for gonad development in females compared to males. Although food intakes (EMI) showed the same trend for both sexes, the lower energy demands in males allow concomitant improvements of both the somatic and reproductive condition, while females allocate most food input to gonad growth, improving their reproductive condition. This would also explain the effect of size on the somatic condition of large-sized (>15 cm ML) animals, which showed a strong increasing pattern for males but was hardly significant for females. In fact, a slowdown of growth during maturation, much more accentuated in females than in males, has been reported in several cephalopod species (Mangold-Wirz, 1963; Boyle and Rodhouse, 2005).

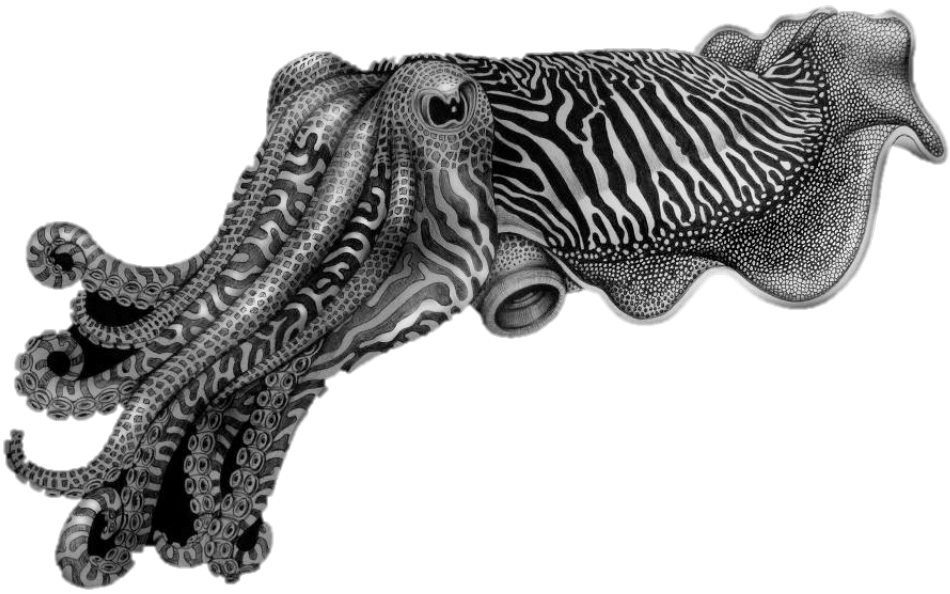
As a result of its high sensitivity to environmental conditions, cephalopods are considered good ecological indicators of both natural and human induced variations in marine ecosystems (André et al., 2010). Most available studies dealing with environmental effects on cephalopod populations analyzed the influence of climatic phenomena at large spatial scales (e.g. El Niño-Southern Oscillation, North Atlantic Oscillation, Mediterranean Oscillation), remotely sensed ocean data (e.g. sea surface temperature, chlorophyll *a*) or local weather-related parameters like rainfall, river discharges and winds (for recent reviews, see Semmens et al., 2007 and Pierce et al., 2008). Cephalopod responses to NAO seem to be species-specific: whereas positive NAO values (high winter temperatures and reduced precipitation over Europe; Hurrell, 1995) were related to high abundances and precocious maturation of *Loligo forbesii* in northeast Atlantic waters (Pierce et al., 2005), negative NAO values were associated with high abundances of *Illex illecebrosus* in the northwest Atlantic (Dawe et al., 2000). In Mediterranean latitudes, the NAO has also been reported to influence fishes (Massutí et al., 2008), crustaceans (Maynou, 2008) and cephalopods (Orsi-Relini et al., 2006). Even the global-scale ENSO index has recently been found to affect Mediterranean cephalopod populations, such as *Sepia officinalis, Loligo vulgaris* and *Octopus vulgaris* (Quetglas et al., 2013). In this study, however, we did not find evidence for an influence of large-scale climatic phenomena such as the NAO, WeMO or MOI on *Sepia* landings. In contrast, the local climatic index (LCI) significantly affected the cuttlefish landings from the Balearic Islands. The influence of the LCI in this area has already been reported for zooplankton (Fernández de Puelles and Molinero, 2007) and benthopelagic fishes such as hake (Hidalgo et al., 2011). Our results also revealed a clear periodicity of about 10 years in the population dynamics of cuttlefish since the early 1980s. There is mounting evidence that the regional hydroclimatic conditions in the western Mediterranean changed noticeably through the 1980s, leading to higher temperatures and hydrographic pressures, less precipitation and weaker winds, which affected the population dynamics of many marine organisms within the trophic webs (Fernández de Puelles and Molinero, 2007; Molinero et al., 2008; Hidalgo et al., 2011; Quetglas et al., 2013). However, the responses to such changes seem to be species-dependent: whereas the shift in the early 1980s induced stronger seasonality in our cuttlefish populations, it in turn led to the disappearance of the seasonality observed for hake until these years (Hidalgo et al., 2009). The high dependence of cephalopods on the environmental conditions, together with their short life cycle and their high adaptability to new ecological scenarios (Pecl and Jackson, 2008), may have triggered the strong change in the monthly landings pattern observed in our results around the early 1980s.

Remotely sensed data have been used in a variety of cephalopod studies and a comprehensive review of cephalopod-environment interactions in European Seas evidenced that the effect of SST varies according to species and areas (Pierce et al., 2008). For example, Wang et al. (2003) found the centre of high squid abundance in the English Channel to be in warmer waters, which is similar to our results of higher availability of cuttlefish at above-average temperatures. Other authors found positive and negative correlations between *Loligo* abundance and SST in the North Sea depending on the season (Waluda and Pierce, 1998). While we obtained a significant positive relationship between SST and cuttlefish landings, no relationship was found for populations from the Gulf of Cadiz (Sobrino et al., 2002). According to Georgakarakos et al. (2002), the correlation of cephalopod abundances with SST depends on the productivity. Although increased food

availability generally has a positive effect on cephalopod growth and abundance (Arvanitidis et al., 2002; Valavanis et al., 2002), we did not find significant relationships between the chlorophyll *a* concentration and cuttlefish landings.

Local weather-related parameters and the moon cycle do not seem to strongly affect cuttlefish populations either. In the Gulf of Cadiz, Sobrino et al. (2002) did not find relationships between trawl landings and rainfall or river discharges. In the western Mediterranean, Lloret et al. (2001) found no or very weak correlations between cuttlefish landings and river run-offs or a wind mixing index. Similarly, our results showed very weak effects of rainfall on weekly landing data from 2000 to 2010. Although there is evidence for lunar influences on some squid species, the results are contrasting and the mechanisms unknown. For loliginid squids, some studies reported increased catches during full moon (Lloret and Lleonart, 2002; Young et al., 2006; Postuma and Gasalla, 2010) but others close to new moon (Schön et al., 2002; Cabanellas-Reboredo et al., 2012). We found effects of both full and new moon, but such effects were marginal compared to the other covariates.

To sum up, our results showed that despite the high sensitivity of cephalopod populations to external abiotic factors, cuttlefish *Sepia officinalis* from the western Mediterranean was not affected by many of the environmental parameters investigated. We only found significant effects of SST and the local climatic index (LCI), whereas no influences were obtained of other parameters such as large-scale climatic phenomena (NAO, MOI, WeMO) or some of the key locally-related variables like rainfall or primary productivity (Chla concentration). This might be explained by the high adaptability of cuttlefish to environmental changes throughout different life stages (Sobrino et al., 2002) and to local hydroclimatic conditions. In fact, our work revealed a shift in the population dynamics during the early 1980s coinciding with important changes in the hydrodynamic conditions in our study area. Finally, we also showed that Mediterranean cuttlefish populations exhibit strong seasonal variations related with the reproductive movements to coastal waters, where the species constitutes an important commercial resource for local small-scale fisheries. In spite of such importance, long term monitoring and fisheries assessment and management in the Mediterranean are missing. Our work is a first step to provide information on cuttlefish life-history and stock dynamics as a knowledge base for future management measures to be implemented in the Mediterranean.



# Chapter 6

# The use of Depletion Methods to assess Mediterranean cephalopod stocks under the current EU Data Collection Framework

# Chapter 6

# The use of Depletion Methods to assess Mediterranean cephalopod stocks under the current EU Data Collection Framework

## 6.1 Abstract

Fuelled by the increasing importance of cephalopod fisheries in Europe, scientists and stakeholders have demanded their assessment and management. However, little has been done to improve the data collection under the EU Data Collection Framework (DCF) in order to analyse cephalopod populations. While the DCF allows member states to design flexible national sampling programmes, it establishes the minimum data requirements (MDR) each state is obliged to fulfil. This study was performed to investigate whether such MDR currently set by the DCF allow the application of depletion models (DMs) to assess European cephalopod stocks. Squid and cuttlefish fisheries from the western Mediterranean were used as a case study. This study sheds doubt on the suitability of the MDR to properly assess and manage cephalopod stocks by means of DMs. Owing to the high plasticity of life-history traits in cephalopod populations, biological parameters should be estimated during the actual depletion period of the fished stocks, rather than performing triennial sampling as established by the DCF. In order to accurately track the depletion event, the rapid growth rates of cephalopods implies that their populations should be monitored at shorter time scales (ideally weekly or biweekly) instead of quarterly as specified by the DCF. These measures would not require additional resources of the ongoing DCF but a redistribution of sampling efforts during the depletion period. Such changes in the sampling scheme could be designed and undertaken by the member states or directly integrated as requirements.

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## 6.2 Introduction

Except for some Mediterranean artisanal fisheries, cephalopods have been traditionally considered as a minor resource for European countries (Pierce et al. 2010). However, in accordance with their increased economic importance around the world during the last decades (Boyle & Rodhouse, 2005; FAO, 2012), some European cephalopod fisheries are now contributing substantially to the economic benefits from the fishing industry (Pierce et al. 2010). Unlike the most important fin fish stocks, cephalopod stocks in Europe are not quota-regulated. Fuelled by the rising importance of their fisheries, scientists, stakeholders and policy-makers throughout Europe have requested for their assessment and management. This requires improving the knowledge of their exploitation status and of the specific tools and data that would be needed for achieving such a goal (Pierce et al. 2010; ICES, 2010; STECF, 2012). Between the late 1990s and early 2000s, the European Commission's Directorate General for Fisheries initiated several studies to develop regular fishery and biological data collection protocols for commercially important cephalopod stocks (Young et al. 2004). The EU Data Collection Framework (DCF) for national fishery data collection programmes (Council Resolution 1543/2000 and

EU, 2008) includes some provision for the collection of biological data and fishery statistics of cephalopods in areas such as the North East Atlantic and the Mediterranean. However, in spite of these efforts, little has been done to assess European cephalopod stocks, and most existing studies have been focussing on the English Channel and Scottish waters (Young et al. 2004; Challier et al. 2005a; Royer et al. 2006; Gras et al. 2014).

Owing to their rapid growth rates and short life-span, little generation overlap and weak or no stock-recruitment relationships, cephalopods cannot be properly assessed by unmodified, standard assessment methods that were initially designed for fin fishes (Pauly, 1985; Pierce & Guerra, 1994). Depletion methods (DMs) have been traditionally used for cephalopod assessment (e.g. Dunn, 1999a; Royer et al. 2002; Robert et al. 2010). During the 1990s, the squid fishery around the Falkland Islands was assessed with this method, and for *Loligo* stocks it is still implemented (Beddington et al. 1990; Agnew et al. 1998, Andreas Winter pers. comm.). Recently, DMs have been used to analyse octopus populations from Moroccan waters (Robert et al. 2010) and the western Indian Ocean (Sauer et al. 2011). In European waters, DMs were applied for the assessment of cuttlefish and squid fisheries from the English Channel and northern Scottish waters (Dunn, 1999b; Royer et al. 2002, 2006; Young et al. 2004; Challier et al. 2005b). The method consists of modelling the depletion of a stock during the main fishing season and analysing the influence of cumulative effort on an abundance index (Royer et al. 2002). This allows interpolation of the total initial stock size during each fishing season (Leslie & Davis, 1939; DeLury, 1947).

Despite the high socio-economical importance of cephalopods in the Mediterranean, only few stocks have been assessed till date. Yield per recruit analysis has been used to assess horned octopus populations from the Ligurian Sea (Orsi-Relini et al. 2006) and cuttlefish from Egyptian waters (Mehanna & Haggag, 2011). Surplus production models have been applied to assess several cephalopod stocks (common octopus, squid and cuttlefish) from the Balearic Sea using a time series spanning more than 40 years (Quetglas et al. 2013).

In the Balearic Islands (western Mediterranean), squids (*Loligo vulgaris* and *L. forbesii*) and cuttlefish (*Sepia officinalis*) are important living resources for local fisheries, which exploit all the three species with both bottom trawl and artisanal fleets. In fact, these cephalopods species had the highest socio-economical impact in the study area (Cabanellas-Reboredo et al. 2011). Squid constitute an important all-year-round by-catch of the bottom trawl fishery working on continental shelf grounds deeper than 50 m, whereas they are caught in relatively smaller numbers by the small-scale fishery (Quetglas et al. 2000, 2014). The two squid species segregate in space and also show contrasting life histories with *L. vulgaris* living on the upper shelf and spawning in spring, whereas *L. forbesii* inhabits the deep shelf and spawns in summer (Šifner & Vrgoč, 2004; Uranga et al. 2012). Contrastingly, cuttlefish supports an important seasonal small-scale fishery (Merino et al. 2008). Artisanal fishers take advantage of the reproductive migration of cuttlefish to coastal waters to catch large, mature individuals using trammel nets during late winter and spring. On the other hand, the trawl fishery catches the recruits in deeper waters during late summer and autumn (Keller et al. 2014 / Chapter 5). In this study, we tested the suitability of the minimum data requirements (MDR) established by the current sampling scheme under the European DCF to assess Mediterranean cephalopod stocks by

means of depletion methods. The conclusions of this study will be used to discuss the possible improvements in data acquisition aimed at assessing cephalopod stocks under the current and future DCFs. Furthermore, the possible use of real time assessments in specific, socioeconomically important artisanal Mediterranean fisheries in order to ensure their sustainable management is discussed. To our knowledge, this is the first application of depletion methods to cephalopod stocks in the Mediterranean.

## 6.3 Material and methods

### 6.3.1 Description of the fishery

Squid and cuttlefish are caught by the bottom trawl and small-scale fleets from Mallorca (Balearic Islands). However, whereas trawlers only catch them as a by-catch all year round, the squid *L. vulgaris* and the cuttlefish *Sepia officinalis* support important seasonal small-scale fisheries. The bottom trawl fleet consists of a rather small number of vessels that has been decreasing gradually over the years (from 41 vessels in 2000 to 32 in 2011; Fig 6.1 A). At the same time, the mean horse power per boat increased slowly from ca. 500 in the year 2000 to about 635 in 2011. The number of small-scale fishing boats decreased from 130 to 119 units while the mean fishing power (in HP) remained more or less constant, suggesting a decrease in the mean fishing effort during 2000–2011 (Fig 6.1B).

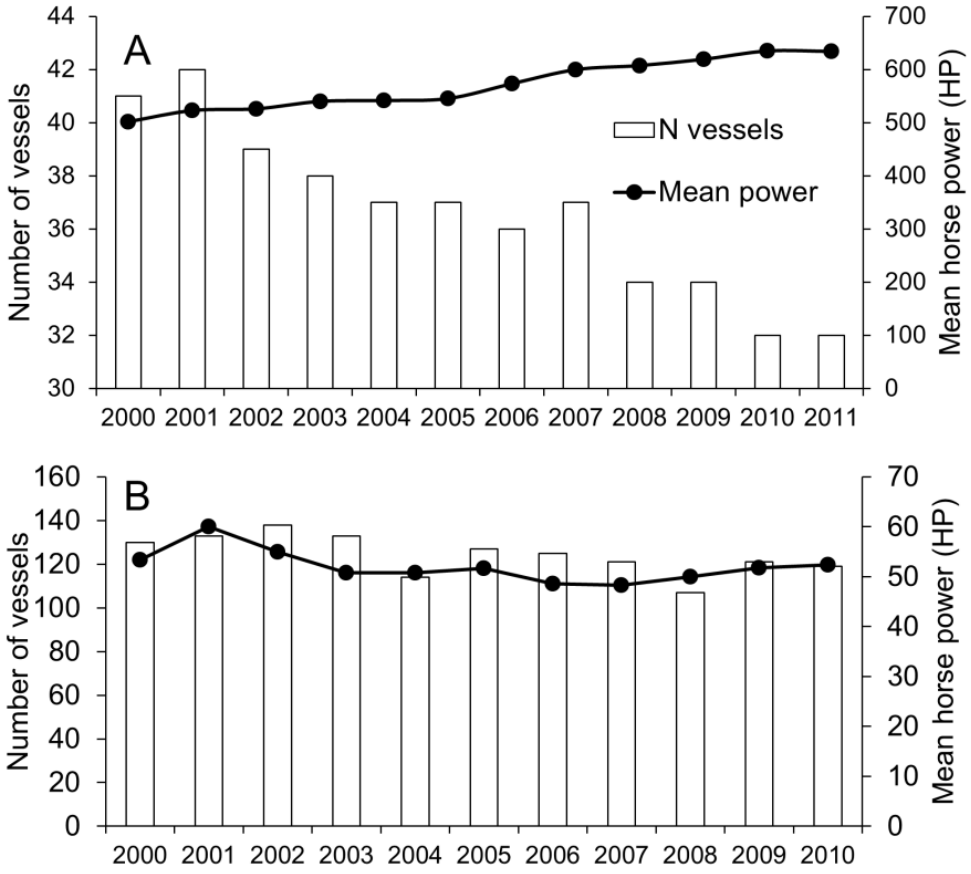



Figure 6.1: Number of vessels and mean horse power (HP) of the bottom trawl (A) and small-scale (B) fleets from Mallorca (Balearic Islands, western Mediterranean).

Most squid landings (Fig 6.2 A) came from trawlers, which showed a clear inter-annual increasing trend from nearly 10 tons (t) in 2000 to 73 t in 2011; landings from the small-scale fleet ranged between 4.7 t in 2008 and 30 t in 2009, with a mean of 11 t in 2000–2011. Trawl and small-scale squid landings show contrasting seasonal trends with maxima in November in the former and July in the latter (Fig 6.2 B). In contrast to squid landings, most cuttlefish landings came from the small-scale fleet and fluctuated between 25 and 56 t during the study period. At the same time, trawl landings of this species ranged from 3.6 to 10 t (Fig 6.2 C). Intra-annual landings of cuttlefish reflect the strong seasonality of its small-scale fishery, which takes place mainly between February and June. Trawl landings decrease progressively from a main peak in February to a minimum in July (Fig 6.2 D).

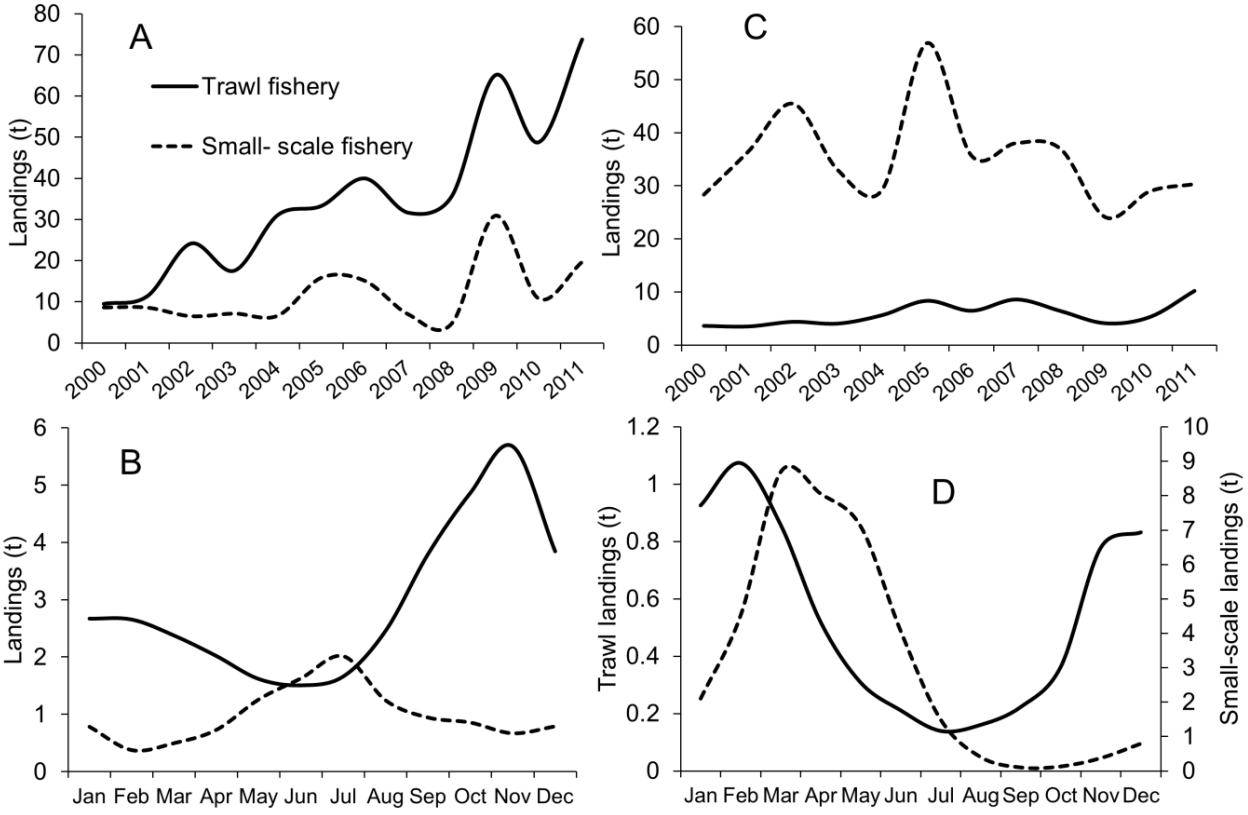



Figure 6.2: Squid (A, B) and cuttlefish (C, D) total annual landings and monthly mean landings (t) of the bottom trawl and small-scale fleets from Mallorca during 2000-2011.

Daily landings per vessel of both the trawl and artisanal fleets of Mallorca were obtained from the fishing auction wharf for the years 2000 to 2011. Since all landings of the island are sold at the same auction wharf, the total landings of Mallorca were available. Furthermore, as discards of squids and cuttlefish are negligible in the area (Sartor et al. 1998), landings represent total declared catches. While cuttlefish landings include a single species (*Sepia officinalis*), two squid species (*Loligo vulgaris* and *L. forbesii*) are commercialized in a pooled category. Therefore, a single combined assessment was conducted for both loliginids, as has been previously done either for the same squid

species in Atlantic waters (Robin & Denis, 1999) and in other fish species that are also sold jointly (Sancho et al. 2003). Biological data (individual size and weight) were obtained from monthly fish market samples analysed at the laboratory. Squid samples were obtained on a monthly basis from the bottom trawl fleet between January and December 2009. A total of 1361 and 643 individuals of *L. vulgaris* and *L. forbesii* were analysed respectively. A total of 806 cuttlefish individuals from the small-scale fishery taken between January and July were analysed monthly for two consecutive years (2007, 2008).

### 6.3.2 Modelling and software

The assessments were conducted using the Leslie-DeLury DMs with the Catch and Effort Data Analysis (CEDA) software (Kirkwood et al. 2003). The following indexed recruitment model was used:

$N_{t+1} = e^{-M} (qCPUE_t - C_t + \lambda R_t)$, where t is the time interval (fortnight), N is the population size in numbers at the start of the time interval t, M the natural mortality rate, q the catchability coefficient, $C_t$ the total catch during the time interval t, λ the recruitment constant of proportionality, $R_t$ the recruitment index and $CPUE_t$ the catch per unit effort during the time interval t.

As CEDA is based on the numbers of animals, the monthly mean weights from the biological sampling were used to convert catches and abundance indices into numbers. As a time interval of two weeks was used for the modelling, weights were interpolated. Although not optimal, this was the best compromise between using the high resolution of the catch data and the lower resolution of the biological data. Length-frequency data was used to calculate the recruitment indices ($R_t$). This index is the proportion of small individuals landed in time t to all small individuals landed during the depletion period, with "small" being below the modal landings modal size (≤10 cm for cuttlefish, ≤9 cm for squid) (Pierce et al. 1994). The model estimates the following parameters: the initial population (N1) and the current stock size, the expected catches for each time step during the depletion event (all in numbers), the catchability coefficient (q), the number of recruits (λ) and a goodness of fit measure ($R^2$). Bootstrapped 95% confidence intervals for q, N1 and λ were also calculated.

CEDA allows specifying three different error models to achieve the best model fit. The least square model assumes independency of the residuals from the expected catch size, whereas in the gamma and the log-transform models, the sizes of the residuals are supposed to depend on the expected catches and are larger when the expected catches are bigger. This relationship between catches and residuals is stronger for the log-transform model than for the gamma one. A preliminary analysis was conducted to analyse the effect of each error model on the results and determine the most suitable one. The goodness of fit of the models was examined by analysing the distribution of the residuals with time. Furthermore, DMs require a constant value for the natural mortality (M) as an input parameter. Previous studies have used M = 0.05 for cuttlefish (Royer et al. 2006) and M = 0.10 / M = 0.835 for squid (Royer et al. 2002; Young et al. 2004). The model's sensitivity to this parameter was checked by applying different homogeneous rates for M (cuttlefish = 0.03, 0.05, 0.07; squid = 0.05, 0.10, 0.12) and comparing the outcomes.

### 6.3.3 Input data and parameters

In each fishing season, only the depletion period was analysed, which is the period corresponding to the time where the CPUE or the catches are declining constantly due to fishing. The time steps chosen for both assessments were periods of two weeks. The biweekly time scale was a trade-off between better resolution of weekly data and monthly availability of the biological data. In both squid and cuttlefish assessments, in addition to the years with available biological data, the two subsequent years were analysed using the biological information from that year.

In cuttlefish, the biweekly landing data of the small scale trammel net fishery from 2007–2010 was analysed and as no biological sampling was performed in 2009–2010, the recruitment indices and mean weights from 2007 were used. For squid, the catches of the bottom trawl fishery from 2009–2011 were analysed. DMs were fitted using mean weights and recruitment indices derived from the biological sampling of commercial landings in 2010 and 2011 (both loliginid species combined). Comparisons with data from on-board sampling showed that the observer programme was not a suitable source of information because of the irregular timing of observations and insufficient sample sizes.

Hilborn & Walters (1992) suggested standardization of CPUE by using a Gaussian error GLM prior to employing them in stock assessment models in order to avoid biases related to spatial, temporal or fleet heterogeneity. Even if the method was successfully used to standardize various stock CPUEs including cephalopods (Royer et al. 2006), it does not deal with zero inflated datasets. To standardize these datasets, the delta-GLM method (which combines a binomial error GLM dealing with presence/absence data and a Gaussian error GLM dealing with abundances) was developed and successfully used in recent years, including cephalopods (Stefansson, 1996; Fletcher et al. 2005; Acou et al. 2011; Gras, 2013). In our study, four variables were considered to standardize CPUE: 1) fortnight period; 2) fishing area; 3) fishing season; and 4) vessel engine power (HP).

## 6.4 Results

GLM-derived abundance indices (standardized CPUEs) showed that the depletion periods span from calendar weeks 15–28 (cuttlefish) and 9–27 (squid); therefore, these periods were used for modelling. The monthly mean weights of cuttlefish derived from the biological sampling of 2007 and 2008 followed a similar pattern in both years with a maximum in March–April (Fig 6.3 A). The calculated abundance index (standardized CPUE) showed a very similar pattern in both years (Fig 6.3 B), whereas the monthly recruitment indices for 2007 and 2008 were very different (Fig 6.3 C). While the index dropped significantly in March 2008 and then increased again until June, in March 2007, it reached its maximum value and only dropped significantly in July of the same year.

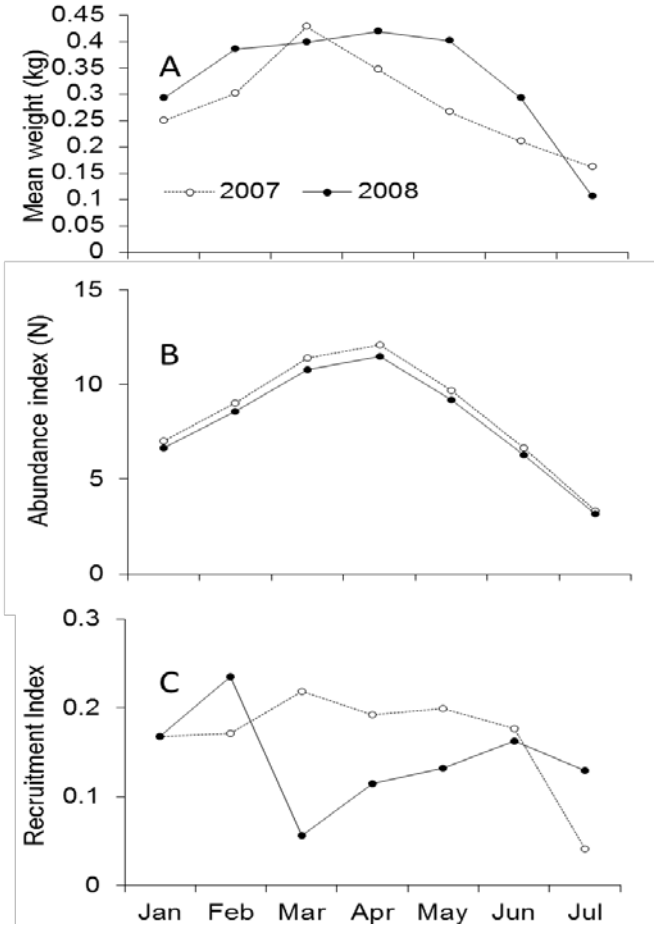



Figure 6.3: Monthly mean weights (A), calculated abundance index (B) and recruitment index (C) of cuttlefish *Sepia officinalis* from the small-scale fleet off Mallorca during 2007 and 2008.

The estimated monthly mean weights of the squid from the biological sampling of 2009 showed a general upwards trend during the analysed period (Fig 6.4 A). The calculated abundance index (Fig 6.4 B) and the monthly recruitment index (Fig 6.4 C) showed a common decreasing trend with time.

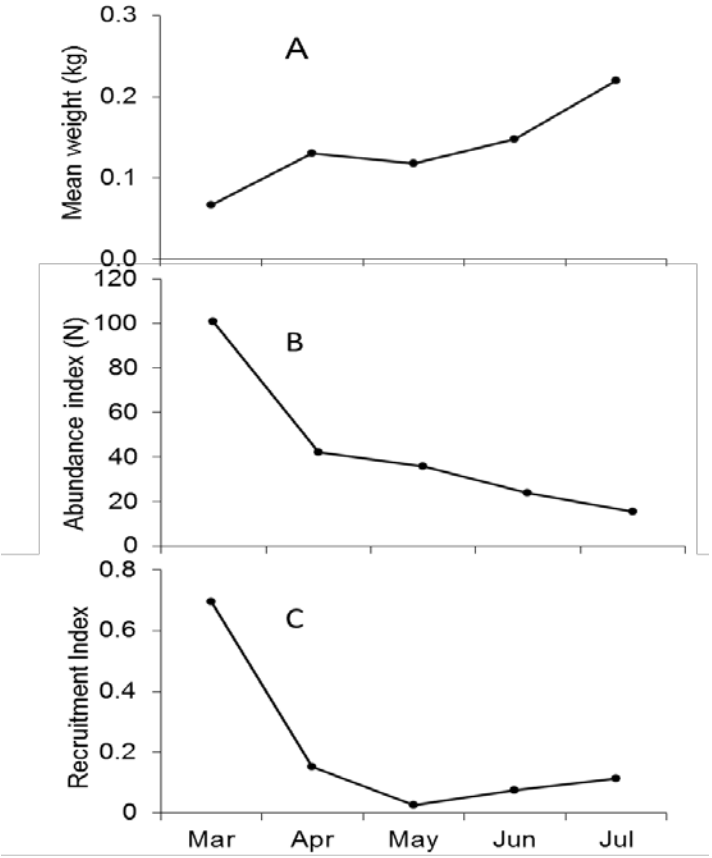



Figure 6.4: Monthly mean weights (A), calculated abundance index (B) and recruitment index (C) of squid *Loligo vulgaris* and *L. forbesii* from the bottom trawl fleet off Mallorca during 2009.

### 6.4.1 Sensitivity analysis

For the *Loligo* data, a model fit was only obtained using a log-transform error model, wherefore it was applied to all depletion periods. Sensitivity analysis conducted using the *Sepia* data for 2007 revealed that all three error models produced very similar results regarding the estimates of original population numbers (N1), numbers of recruits (λ) and final population size (Fig 6.5).

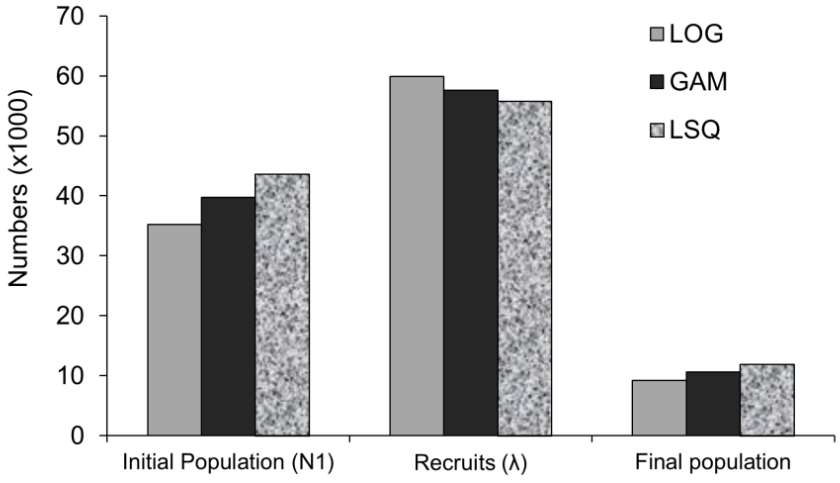



Figure 6.5: Expected initial population (N1), number of recruits (λ) and final population (all in numbers) of cuttlefish from Mallorca using different error models (LOG: log-transformed; GAM: gamma; LSQ: least square).

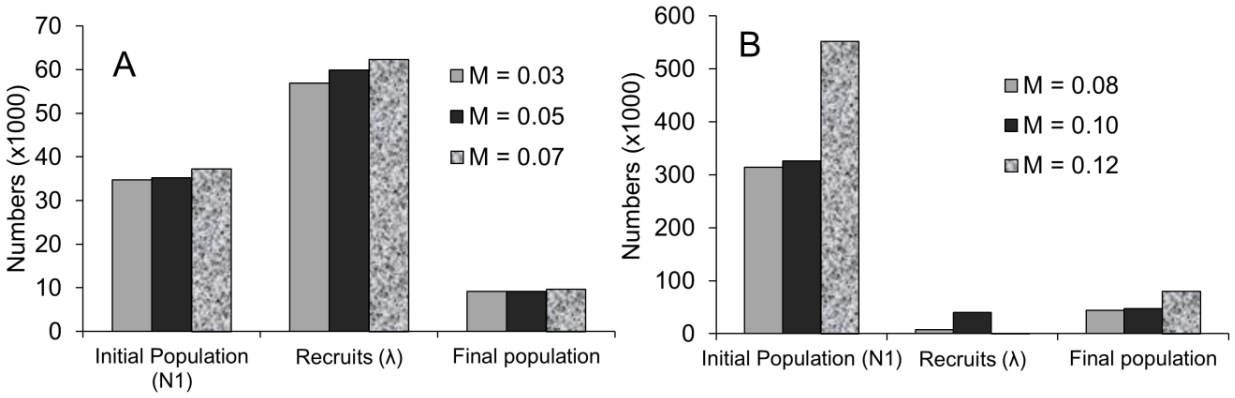



Figure 6.6: Sensitivity analysis testing different natural mortality values (M) for cuttlefish (A) and squid (B) populations from Mallorca. The estimated initial population (N1), number of recruits (λ) and final population (all in numbers) obtained using the log-transformed error model are shown.

Regarding the model's sensitivity to different mortality rates M, the cuttlefish model was not very sensitive (Fig 6.6 A), a result that is in accordance with former studies (Basson et al. 1996; Royer et al. 2006). In *Loligo*, employing an M of 0.12 led to about 1.5 times the initial population number and nearly double the final population, whereas changes between M = 0.08 and M = 0.10 were minimal (Fig 6.6 B). Based on these results, the median values also used in previous studies were used in all further analyses.

### 6.4.2 Model output

In both cuttlefish and squid assessments, fits for all periods were only obtained by using the log-transform model. Regarding cuttlefish, model fits were obtained for all years except 2008, and the parameter estimations differed widely between years, notably for recruits. The initial population (N1) varied between 26,000 and 103,000, and the final population was estimated between approximately 4,000 and 23,000 individuals. The number of recruits (λ) estimates varied between 400 and 59,000. Estimated and observed CPUE were very similar and ranged between 2.2 and 13.4 individuals per unit effort (days at sea), with notably higher total values in 2007–2008 than in 2009–2010 (Fig 6.7 A). Biweekly population numbers versus total catches are given in Figure 6.7 B. Catches showed similar ranges in all three years with model fit (2007, 2009, 2010), but the pattern found in 2009 differed compared to the rest. Population numbers were much higher and declined more abruptly with time in 2009 than in 2008 and in 2010.

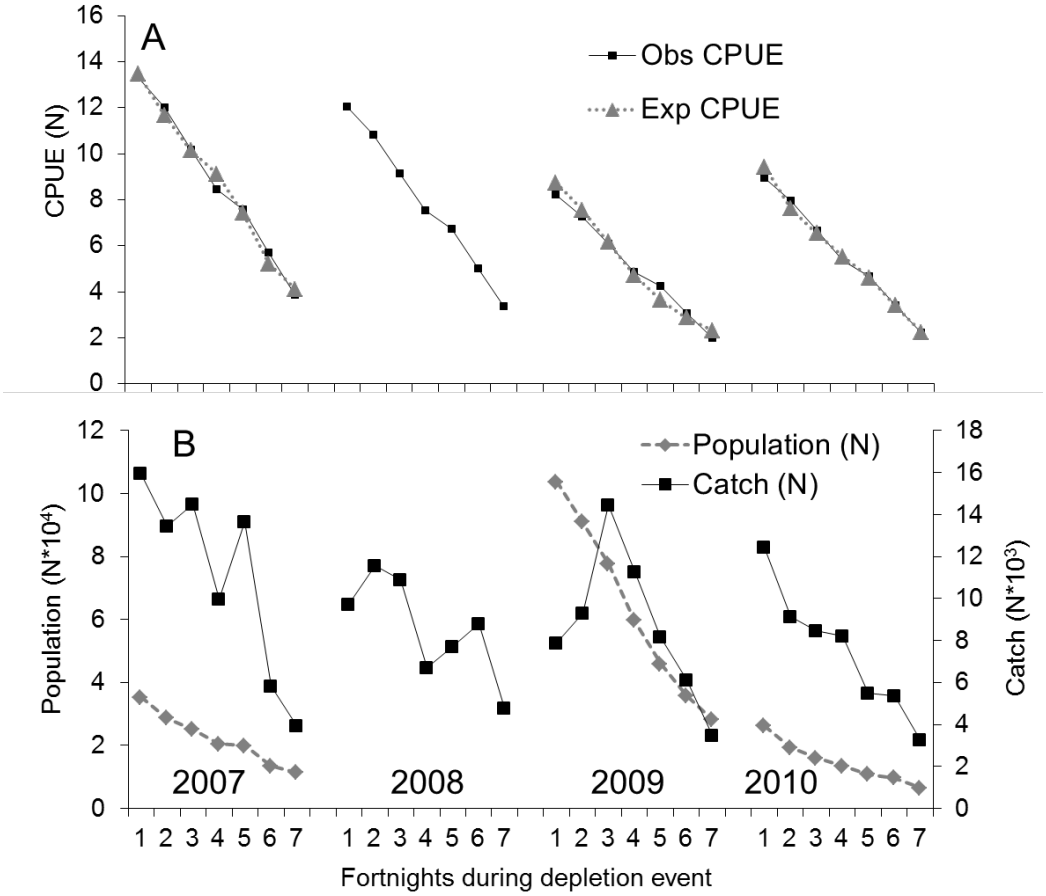



Figure 6.7: Observed and expected biweekly CPUE (A) and stock size and catch (B) of cuttlefish *Sepia officinalis* from the small-scale fleet off Mallorca during 2007-2010 using M=0.05. Fortnights 1-7 correspond to calendar weeks 15-28.

In the case of the loliginids, model fits were obtained for all the three years (2009–2011), and the model estimates differed less than for cuttlefish (Fig 6.8). The initial population (N1) varied between 326,000 and 440,000 animals, and the final population between around 44,000 and 71,000 individuals. Apart from the first fortnight, estimated and observed CPUE were again very similar (Fig 6.8 A). Biweekly population numbers (estimated) start at approximately 30% higher in 2011 than in 2009 and 2010, and total biweekly catches (numbers) showed a different pattern every year (Fig 6.8 B).

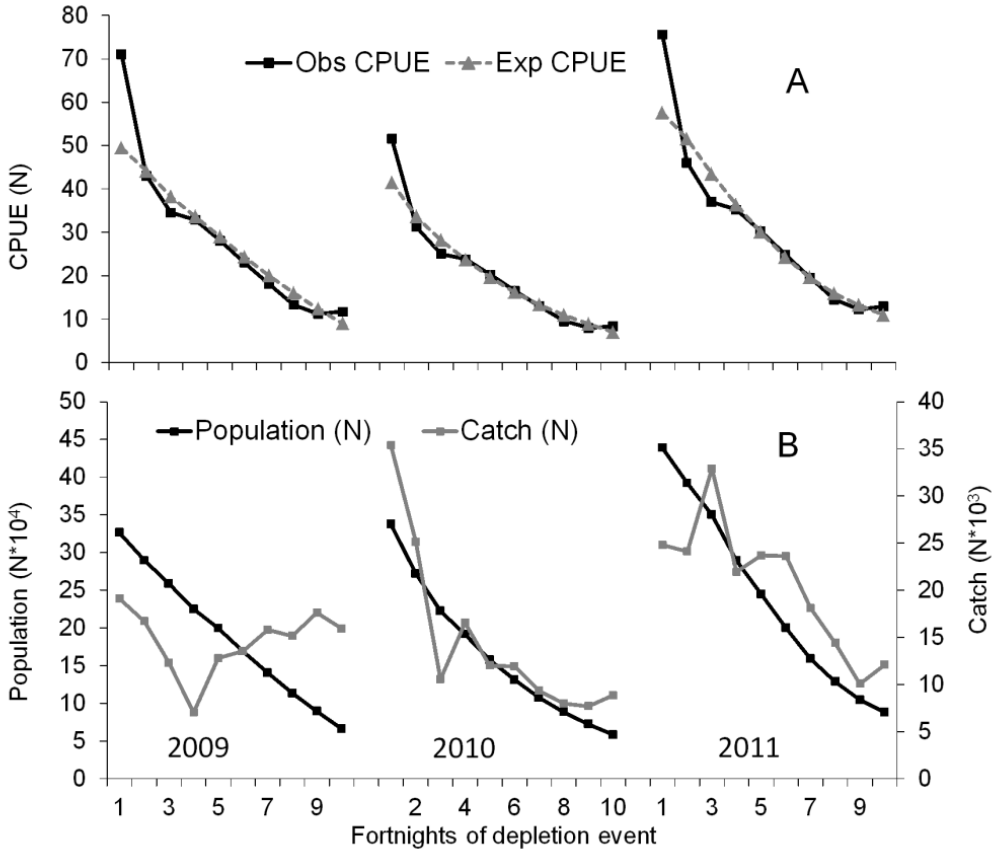



Figure 6.8: Observed and expected biweekly CPUE (A) and stock size and catch (B) of squid *Loligo vulgaris* and *L. forbesii* from the bottom trawl fleet off Mallorca during 2009-2011 using M=0.1. Fortnights correspond to calendar weeks 9-28.

## 6.5 Discussion

The assessment and management of cephalopod stocks is of great relevance owing to the socio-economically important fisheries they sustain worldwide and the pivotal role they play in marine food webs (Boyle & Rodhouse, 2005; ICES, 2010). Despite previous demands from both European scientists and fishing organisations to improve data collection for cephalopod assessment (Young et al. 2004; ICES, 2010, 2011, 2012), little has been done under the EU Data Collection Framework (DCF) till date. While member states have been given the flexibility to design their own national sampling programmes in line with the community programme, the DCF establishes the minimum data that countries must acquire and report to the EU Commission.

Under the current DCF (EU, 2010), collection of biological information includes metier- and stock-related variables. In the first case, sampling must be performed to evaluate the quarterly length distribution of species in the catches and the volume of discards for each major fishing metier. In the second case, the sampling scheme requires individual information on length, weight, sex and maturity to be gathered every three years for each specified species. According to the current DCF, the sampling of stock-

related variables of cephalopods in European waters is mandatory in only two main regions, the North East Atlantic and Western Channel (NEA-WC) and the Mediterranean and Black Seas (MS-BS). In all other European areas (North Sea and Eastern Channel, Baltic Sea, Skagerrak and Kattegat), the DCF does not include any cephalopod species. In the NEA-WC, three cephalopod species are to be sampled: the common squid (*Loligo vulgaris*), the common octopus (*Octopus vulgaris*) and the cuttlefish (*Sepia officinalis*). Because of the importance of cephalopods for Mediterranean fisheries, however, the following species were added to the three previous ones in this sea: the horned octopus (*Eledone cirrhosa*), the musky octopus (*Eledone moschata*), the southern shortfin squid (*Illex coindetii*) and the European flying squid (*Todarodes sagittatus*).

According to the current view, DMs may be considered the most suitable methods for cephalopod assessment (e.g. Royer et al. 2002; Robert et al. 2010; Rodhouse et al. 2014). In this study, we investigated if the information currently demanded by the DCF allows the application of such methodology to properly assess the European cephalopod stocks. Owing to their rapid growth rates, cephalopods display high plasticity in life-history traits (Boyle & Rodhouse, 2005; Pierce et al. 2008). Substantial changes in biological parameters in cephalopods are well-documented and reflected at different time scales encompassing years (Pecl et al. 2004; Smith et al. 2005), seasons (Jackson et al. 1997; Pecl, 2001; Jackson & Moltschaniwskyj, 2001), weeks (Jackson & Pecl, 2003) and even days (Moltschaniwskyj et al. 2002). All these studies indicate that biological parameters of cephalopods should be estimated at shorter time scales during the actual assessment period, invalidating the triennial sampling scheduled by the DCF, which is clearly not adapted to short-living species like cephalopods. Results of cephalopod stock assessments by means of DMs are, in fact, in agreement with this idea of more regular sampling. Indeed, strong and significant inter-annual differences in average monthly body weights in squid populations from Scottish waters were found (Young et al. 2004).

Our results showed wide inter-annual variations in recruitment and population size, which seemingly are not linked to changing fishing activities owing to the short time period analysed (3–4 years). Such high variations seem to be inherent to cephalopod stock modelling using DMs, as they have been observed in most studies published till date (e.g. Agnew et al. 1998; Royer et al. 2002, 2006; Young et al. 2004). In the English Channel, for example, the initial population size of squid ranged between 49,000 and 6,000,000 individuals (M = 0.2) and the recruitment numbers at the beginning of the depletion period ranged between about 1,000,000 and 2,100,000 individuals. For cuttlefish, annual recruitment varied between 44,000,000 and 79,000,000 (Royer et al. 2006). Significant annual variability is also evident in the recruitment indices of Mediterranean cuttlefish, which were markedly different in 2007 and 2008 (Fig 6.3 B). Although these wide inter-annual variations might be reflecting the aforementioned plasticity of cephalopod populations, the fluctuations seem unrealistic in some cases and raise concerns of poor data quality or compromised model assumptions, as discussed below.

Regarding data quality, a distinction has to be made between fishery statistics (landings and effort) and biological (mean weights, reproductive index) data. In contrast to previous decades, most Mediterranean EU countries nowadays have reliable time series of catch-effort data gathered under the DCF. Having daily catch and effort data is a big improvement and could supply data of weekly mean weights if landings were sorted out

by commercial categories, as proposed previously (Royer et al. 2002) and already been used in some cephalopod stock assessments (Jouffre & Caverivière, 2005). The impediments noted by previous authors (Young et al. 2004), such as no reporting of artisanal fishery or misreporting, was not a concern in our case. There is little missing data or hidden catches regarding cephalopod statistics, as there are no set total allowable catches (TACs). Problems arise only when a single commercial category includes several species, as is the case with our squid data that comprises of two species (*Loligo vulgaris* and *L. forbesii*) with different spawning and recruitment periods (Robin & Denis, 1999; Denis et al. 2002). While some EU regulations specifically demand additional biological sampling for the purpose of getting species proportions in such cases, these are still missing in several statistics and national sampling programmes (ICES, 2010).

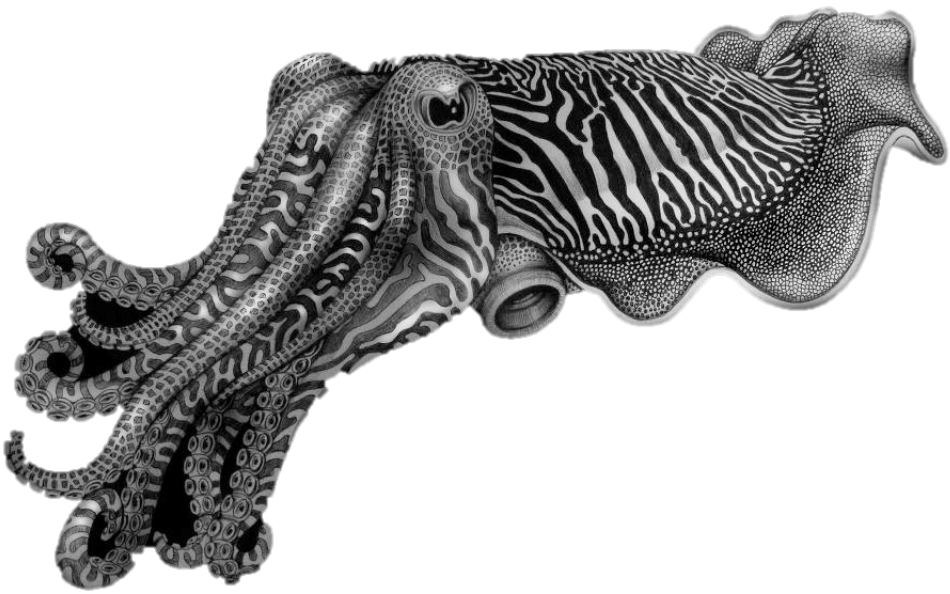
The model assumptions include a closed area, a constant catchability over stock size and time, and no target switching by fisherman within time. Both loliginid squid and cuttlefish undertake seasonal migrations, which lead to temporal, local accumulation or disappearance of the animals and therefore violate the model assumptions of a closed area and constant catchability (Arkhipkin et al. 2013). In contrast to the Falkland Island fishery, where the animals are caught prior to their reproductive migration (McAllister, 2004), the Mediterranean small-scale fishery focuses on cuttlefish (Keller et al. 2014 / Chapter 5) and squid (Cabanellas-Reboredo et al. 2012) at their breeding grounds; which is the reason for excluding the period of initial arrival to the fishing grounds in our models. Furthermore, the emigration of big animals from the spawning area can lead to the sampling of different parts of the population at different times (Mangold-Wirz, 1963). When the mean weights drop for this reason, catches in numbers will increase and result in a seemingly slower depletion of the stock than actually happening. However, a depletion analysis of the English Channel loliginid squid stock gave similar outcomes regarding the total stock and recruitment size, and so did the virtual population analysis they conducted (Royer et al. 2002). Therefore, the applied method seems to be valid. Another possible source of error arises from the parameter estimates, such as the natural mortality (M), which cannot always be determined with certainty (Wang & Liu, 2006; Jiao et al. 2012). Furthermore, the semelparity of the species will lead to a change in the natural mortality rate after the spawning period, and some of this variability might already be reflected within our study period. Nevertheless, as revealed by our own results and also by previous studies (Royer et al. 2002, 2006; Young et al. 2004), DMs are quite robust to changes of M within the ranges tested.

Whereas the first EU framework (Council Regulation 1543/2000) was established at the stock level, by focusing on the most important commercial species, the current one (EU, 2010) is based on the so-called concurrent sampling, that is, sampling all or a predefined assemblage of species simultaneously in a vessel's catch or landings. Assessing cephalopod stocks by means of DMs requires intense sampling at low temporal scales (weekly or biweekly) to properly track the depletion event. To optimize the sampling of cephalopods for assessment purposes under the DCF, this should be concentrated during the relatively short period of the depletion event each year, which is the only relevant period for the required data of individual sizes and weights.

In conclusion, the trials conducted in this work shed doubt on the suitability of the minimum data requirements of the DCF to properly assess and manage Mediterranean

cephalopod stocks with depletion methods. The suggested improvements in the sampling design would make the assessment of cephalopod populations in European waters more efficient and accurate. Considering the high importance of cephalopod fisheries in the Mediterranean, such improvements are especially relevant in these waters. In 1999, for instance, approximately 80% of the total world catch of cuttlefish came from this area, whereas the Mediterranean octopus landings ranked third, after the comparatively larger western and eastern central Atlantic FAO areas (Boyle & Rodhouse, 2005). In most cases, cephalopod fisheries are seasonal and the catches reach high prices. Besides the fisheries analysed in this study, it is worth mentioning the fishery for juvenile *Eledone cirrhosa* in some areas of Spain (Sánchez et al. 2004) and Italy (Belcari & Sartor, 1999), where the prices of the smallest individuals can exceed 200 €/kg.

In such valuable fisheries, real-time assessments using depletion methods might be useful and have already been applied in the squid fishery from the Falkland Islands (Agnew et al. 1998; Arkhipkin et al. 2013). The assessment and management system used in this area makes it one of the best-managed squid fisheries in the world, with effective cooperation between scientists, managers and stakeholders to assure sustainable, long-term resource exploitation (Arkhipkin et al. 2013). The Falkland Islands squid fishery is managed using a combination of effort control (a limited number of vessels are licensed to fish during each of two open seasons), a recruitment biomass survey before each commercial season and an in-season assessment of the state of the stock in relation to biological reference points, such as minimum levels of spawning stock biomass (Agnew et al. 1998; Arkhipkin et al. 2013). The stock size is then monitored in real time using DM assessments, and the fishery may be closed early to preserve a target escapement (Agnew et al. 2002). Although the authors do not suggest the adoption of this complex, long-standing assessment scheme in Mediterranean waters, the issuing of licenses, together with in-season monitoring and post-season assessment, may be useful to ensure sustainable harvesting of the stocks. The high multi-specificity of most Mediterranean fisheries would likely preclude the effectiveness of this scheme, but it may be applied to the aforementioned high-valued artisanal fisheries, which are monospecific fisheries targeting a single cephalopod species. Post-season assessment in the remaining fisheries, however, might be useful to detect midterm trends and also to better understand the behaviour of fishing fleets in reaction to recruitment variations. As a result, Mediterranean fishers might reallocate the fishing effort towards alternative resources during periods of low recruitment using its flexibility to exploit different grounds even on a daily basis (Palmer et al. 2009).



# General discussion

# Conclusions

# References

# General discussion

## 7.1 Synthesis

This thesis integrates knowledge of cephalopod population dynamics and community patterns at different spatial and temporal scales. While a detailed discussion of each topic can be found within each chapter, this discussion aims to synthesise the main contribution of this thesis as well as the implications of the obtained results for future ecosystem conservation and fisheries management. It will also give some perspectives of the putative consequences of future climate change scenarios on observed cephalopod abundance and distribution patterns. Furthermore, possible shortcomings of the presented works, potential extensions and further avenues of research are discussed.

Nowadays, fishery management of single species is considered little effective in many cases, as it does not take into account side-effects of the fishery, like habitat destruction, mortality of bycatch species, or ecosystem changes. Furthermore, it is often based on assumptions that do not always hold true, as for example constant natural mortality, equilibrium state or negligible species interactions, among others (Francis et al. 2007). Therefore, in the last two decades, a paradigm shift has been seen in fishery science. The present approach, the **Ecosystem Approach to Fisheries Management (EAFM)**, has a much wider perspective (Longhurst, 2006), and while it integrates single stock assessments, it does not rely exclusively on it. The EAFM aims – amongst others - to prevent the degradation of ecosystems, to reduce changes in species composition and ecosystem processes and to gain knowledge about these processes, in order to evaluate possible consequences of human impacts (Hilborn, 2004; Jennings, 2004; Pikitch et al., 2004; Pennino, 2013). This approach, which takes into account habitat as well as prey-predator and other interactions, requires much more information than a single species approach. Advanced models should account for spatial structure and environmental processes and this requires previous studies at population, community and ecosystem level (Pennino, 2013). As species distribution and dynamics are often governed by large-scale environmental processes and long-term fluctuations (Hughes et al., 2005; Molinero et al., 2005; Chen, 2010; Piroddi et al., 2015b), studies are needed at these large spatio-temporal scales. Only this way, a wider and more complete picture of the ecosystem in question can be obtained (Pennino, 2013). With the additional information of different ecosystem compartments, more integrative reference points can be developed and models and management tools will be improved.

The first section of this thesis, therefore, focuses on these broader spatio-temporal scales, using a faunal group of paramount importance at ecosystem level, the cephalopods. This animal group has proved to influence population abundances in their preys (Alarcón-Muñoz et al., 2008) and predators (Barlow and Forney, 2007), and may even affect the breeding success of their predators (Xavier et al., 2007). Their impact on marine communities and fisheries can therefore be substantial (Field, 2008), highlighting the importance of detailed knowledge of this group at species / community level. As a starting point, chapter 2 deals with community structures at large scale, and investigates the influence of large-scale environmental gradients on cephalopod species composition and

community structure in the two Mediterranean sub-basins. While no differences in species composition have been found, relative species contributions differ in the two basins. The chapter further analyses important drivers of cephalopod assemblages, revealing slightly different mechanisms for each basin. Another important pillar of the EAFM is the characterization and conservation of the ecosystems resilience (Francis et al., 2007), which in turn depends strongly on the biodiversity of the system (Hughes et al., 2005). Thus, the work presented in chapter 3 supplies information on cephalopod diversity at large temporal and spatial scale and constitutes an important contribution towards improving our integrative knowledge of the Mediterranean ecosystems. Results reveal the absence of clear longitudinal or latitudinal gradients in cephalopod diversity, combined with no distinct temporal trend over the last two decades. Depth, sea surface temperature (SST) and productivity regime (Chl *a* content, Chla) resulted to influence the cephalopod diversity. Spatially speaking, these results are equatable with those obtained in the chapter 4, which investigates the long-term trends and synchronies in population dynamics of two commercially important cephalopod species. As the strength and nature of the synchrony among populations affect the abundances, resilience and recovery of connected populations, results have important implications for their management. Especially the regionalisation process contemplated under the new Common Fisheries Policy (CFP; EU-Regulation Nº 1380/2013) can certainly benefit from the new insights, as population sub-structuring across the Mediterranean Sea were revealed. This chapter also reveals how environmental variability, SST and surface primary production contribute to the spatial structuring of cephalopod populations.

Chapters 2-4 investigate the large-scale variability of the cephalopod communities from three complementary perspectives: community structure and biodiversity, and spatio-temporal patterns of key species. The results of these studies evidence recurrent patterns at the Mediterranean scale: the difference between processes in the Eastern and Western sub-basins, and the influence of SST and productivity on cephalopods at species and community level. In chapter 2, the importance of SST and productivity in structuring communities varies between sub-basins, pointing to different processes operating in the two areas. This result is supported by the observation that abundances of the common octopus *Octopus vulgaris* and the broadtail squid *Illex coindetii* show a common trend in the eastern sub-basin but contrasting trends among different geographical locations (GSAs) in the western sub-basin (Chapter 4). Another common result is the influence of SST and productivity on community patterns, diversity and abundances. Our findings that *I. coindetii* abundance and distribution are negatively influenced by high productivity and low spring temperatures (Chapter 4) are supported by the results of the community analysis (Chapter 2), where the presence of squid in the eastern basin is fostered by low productivity regimes and high spring SST. Consistent effects of these environmental gradients on community properties such the biodiversity (Chapter 3) evidence the high influence of large-scale variability on populations and community structure of cephalopods across the entire Mediterranean Sea.

The Marine Strategy Framework Directive 2008/56/EC (MSFD) is the main European directive on marine waters nowadays. The Framework requires the assessment of all European seas at regional scales in relation to their ecosystem status and associated pressures to achieve “Good Environmental Status” by 2020 (Cardoso et al., 2010; Piroddi et al., 2015a). In the Mediterranean, a shift has been observed in the food web structure of the ecosystem from 1950 to 2000, where benthic and benthopelagic cephalopods have

substituted medium-sized pelagic fishes in importance (Piroddi et al., 2015a). The knowledge of cephalopod community structure (Chapter 2) is therefore relevant for the assessment of the ecological status of this sea. The time-series analysis of diversity indices in chapter 3 supplies additional information on the temporal diversity patterns. The fact that no clear diversity trends have been observed in the last 20 years complements our snapshot of the community composition averaged on 6 years. As community characteristics like species composition and diversity do not allow discerning trends at species level, the last broad-scale analysis (Chapter 4) focuses on the abundance data of two model cephalopod species (benthic and pelagic) and evidences influences of environmental parameters at species level.

While chapters 2-4 are based on large spatio-temporal scales and may improve modelling and supply information for EBFM, the chapters 5 and 6 focus on small scale, local ecological processes at short time scales and supply more hands-on information that can be directly implemented by local managers. The motivation for these chapters was fuelled by the present situation in the Mediterranean Sea, where cephalopod stock assessments are far from being implemented, despite their importance for ecosystem functioning and as commercially valuable resources. Given these circumstances and the rising fishing pressure on cephalopod stocks worldwide, there is concern that overexploitation of cephalopod stocks is already reality, a hypothesis supported by the fact that world cephalopod landings have peaked in 2007 and steadily declined since then (Rodhouse et al., 2014). In the Mediterranean, this group might therefore experience the same overexploitation as commercial fish (Quetglas et al., 2015). Fish stocks are broadly depleted in the Mediterranean, and no current management has succeeded in restoring these stocks and protecting current resources yet (Vasilakopoulos et al., 2014). The fact that – different than in fish – no European country has integrated the assessment of cephalopod stocks in its national fishery policy may cause delayed realisation and contra-measures when it comes to their depletion. Given their dependence on the success of only one generation, depletion of their stocks may also have severe consequences for their predators, which may be protected species (Aydin 2002) or other valuable fishery resources (Hunsicker et al., 2010).

Given this background, local fishermen and management agencies shall be interested in the conservation and sustainable exploration of economically important cephalopod species. In the case of the Balearic Islands, one of them is the cuttlefish *Sepia officinalis*. The detailed information in chapter 5 about the cuttlefish's life-history, dynamics and biology, as well as influencing factors, are therefore of high interest for the stakeholders. The short-term and intra-annual data used may uncover important processes and drivers they need to take into consideration in sound management. While the chapter provides a complete view of the intrinsic and extrinsic drivers of the cuttlefish population fluctuations in the Mediterranean Sea, the following study (Chapter 6) represents the next step, applying stock assessment techniques to cuttlefish and squid fisheries. Being the first application of depletion methods to Mediterranean cephalopod stocks, it uncovers existing problems and questions the applicability of the current sampling scheme in view of the assessment´s data requirements. Consequently, a modification of the existing scheme is proposed. Results are of special interest to local policy makers, but may even be of national or international interest, as cephalopod assessment is still neither implemented in any Spanish region nor elsewhere in the European Union. Relatively little scientific effort has therefore been dedicated to this field in Europe. For this reason and their special life-history

traits, tools for cephalopod assessments are still less developed, applied and useful than those currently available for fish. Therefore, our results may improve the current situation and support better and more accurate management strategies.

Indeed it has been hypothesised that the inclusion of environmental variability in modelling and management plans may preclude unpredicted oscillation in landings (Hunsicker et al., 2010). In other words, oceanographic conditions that influence cephalopod dynamics should be considered by fisheries managers to improve forecasts (Agnew 2005, Waluda 1999). The influence of the Local Climatic Index (LCI) around the Balearic Islands and the shift in the seasonal dynamic of cuttlefish as revealed in chapter 5 may therefore be of value to embrace environmental variability in future assessment. In this context of fishery management, chapter 6 considers assessment issues from a different angle, focusing on one specific methodology and evaluating the input data obtained from biological sampling. It shows that the implementation of depletion methods still produce insufficient results given the currently inadequate sampling scheme under the Data Collection Framework (DCF). In conclusion, this section of the PhD illustrates that different aspects have to be considered and should be improved for successful modelling, prediction and management of cephalopod stocks.

## 7.2 Perspectives under climate change

The climate change scenarios of the fifth report of the Intergovernmental Panel on Climate Change (IPCC) predict rising temperatures and changed productivity regimes. According to the modelled scenarios, and assuming that cephalopod diversity is mostly governed by the productivity regime (Chapter 3), it may decline in the entire Mediterranean Sea. The expected temperature rise, on the other hand, would cause rising species richness, according to our results of chapter 3. The unknown will be which process, temperature or productivity, exert the stronger influence on the regional diversity. According to Macias et al. (2015), climate change probably leads to different outcomes in the two Mediterranean sub-basins: while primary production may rise in the eastern basin, the western basin will more likely be characterised by decreasing Chla concentrations. When linking these models to our results of chapter 4, the abundances of *I. coindetii* and *O. vulgaris* may suffer a decline in the eastern basin, while they may rise in the western. These outcomes are still very speculative though, as future projections are very difficult to make, given that any external change will affect different species and even different life stages in different ways (Pecl and Jackson, 2008). While early life stages will probably be negatively affected on a physiological basis, the abundance and distribution of adult cephalopods is governed by different processes, and the combination makes predictions rather difficult (Pecl and Jackson, 2008; André et al., 2010). Furthermore, cephalopod species with planktonic life stages are presumed to be more effected by the predicted changes in seawater chemistry, oceanography and plankton abundance (Poloczanska et al., 2007). And even stocks of the same species can react in different ways at different locations (Tian, 2009). Given the results of ours and other studies on this topic (Pecl and Jackson, 2008; André et al., 2010; Kaplan et al., 2013) and the sensibility of cephalopods to environmental changes (Pierce et al., 2008; Rodhouse et al., 2014), it is almost certain that cephalopods in the Mediterranean Sea will react in one way or another in the close future. And being keystone ecosystem species, this may in turn have profound impact on the Mediterranean ecosystem as a whole.

## 7.3 Possible shortcomings and future research needs

While some limitations in the presented studies result from time and money constrains as well as insufficient data, others result from missing knowledge which may be available for future research. Therefore, limitations and desirable further investigation topics are discussed together in this section. First, satellite data of productivity and temperature are only available at surface level. This gives an approximation of the environmental conditions, but not always realistically mirrors the conditions single species are surrounded with. This is true especially for benthic oceanic species. Furthermore, satellite data time series are of limited length, being a relatively modern resource. Our models including environmental drivers were therefore shortened according to this time frame, even though biological data existed for many more years. Regarding data limits, I must mention the importance of other factors that could be included in the modelling and would most probably improve its explaining power. These are certainly information on fishing pressure and characteristics of the fisheries, predation pressure (Staudinger 2013), resource / prey availability and seabed characteristics. Salinity data as well as information on shelf extension and historical events may probably improve the modelling results as well. Although some of these data are available in some areas, they are absent in others, and the integration of all this information for the whole study area of the Mediterranean Sea would have been very challenging. Given these data restrictions, in the first part of the thesis (Chapters 2 - 4) we decided on a compromise of simpler models with available environmental drivers but large spatio-temporal scales. Studies of larger scale are more inclusive (especially dealing with mobile species showing fluctuating population dynamics) and able to supply different information than the already existing small-scale ones.

Regarding the local analysis of Balearic fisheries (Chapters 5 and 6), problems vary from insufficient input-data due to the currently insufficient sampling scheme to general knowledge gaps regarding cephalopod populations and movements. Population studies and stock assessment need precise input data on the abundances of the species in question; this makes knowledge on stock boundaries crucial. Unfortunately, this information is often missing, and further studies are needed in this field. In our case, these studies will have to investigate the connectivity between Mediterranean cephalopod populations and may include studies on larvae dispersal, genetics, or tracking (Perez-Losada et al., 2007; Semmens et al., 2007; Cabanellas-Reboredo et al., 2012). More importantly, an intrinsic problem of cephalopod research is their characteristic mating and spawning migration (Semmens et al., 2007). These migrations are problematic when it comes to the modelling of cephalopods abundances, population dynamics and consequent management, as the displacement creates important variations in their spatio-temporal distribution (Wang et al., 2003; Boyle and Rodhouse, 2005; Roberts et al., 2012). This, in turn, determines their vulnerability to fishing. Depending on the timing and on the percentage of the population that migrates, different modelling and management tactics are needed, as potential threads to their population will either result from the artisanal fleet (where existent) or the commercial trawl fishery. Further research in this area shall greatly improve current assessment and management and could include tacking indirect measures like genetic studies, chemical tracking and satellite data analysis of fleet movements (Semmens et al.,

2007). The gained information should then be integrated in current stock assessments, as for example developed by Basson et al. (1996).

A more specific problem is associated with the assessment of *Loligo* species. *Loligo vulgaris* and *Loligo forbesii* mostly inhabit different depth and exhibit different spawning and recruitment periods. Their stocks should therefore be treated separately when it comes to fisheries management. Nevertheless, in Spanish and most other European statistics, the commercial category of *Loligo* catches contains at least two species (Pierce et al., 2010). A future improvement of the data situation would be the separation of *Loligo* catches at species level or the development of species proportions of a given fishing ground.

Finally, another important element to enhance assessment's effectiveness in fisheries management is the integration of the recreational fishery, as done in some commercial finfish fishery already (Coleman, 2004; Lynch, 2006; Post et al., 2008). As of 2009, the European Union legislation recognizes this important issue and requires surveys of recreational fishing activities to obtain better estimates on the volume of these fisheries (Council Regulation EC 1224/2009; Piroddi et al., 2015a). Recent research on the recreational squid fishery in the Balearic Islands evidences its importance and possible integration into current assessment (Cabanellas Reboredo, 2014).

# Conclusions

1. In spite of contrasting oceanographic conditions between the western and eastern Mediterranean sub-basins, demersal cephalopod assemblages showed the same species composition, though they differed in relative species contribution.

2. Bathymetry was confirmed to be the most important structural driver of cephalopod assemblages in both Mediterranean sub-basins, revealing three different communities corresponding to the continental shelf and the upper and middle slope.

3. Community composition was further influenced by sea surface temperature (SST) and productivity regime (Chlorophyll *a* concentration, Chl *a*).

4. Effects of SST and Chl *a* were generally time-lagged by about 6 months. Community composition showed a stronger influence of temperature in the western than in the eastern basin, while Chl *a* showed a consistent, but less important impact in both basins.

5. SST and Chl *a* also influenced the cephalopod diversity throughout the whole Mediterranean, together with depth and additional regional processes.

6. High SST values influenced diversity positively, while a dome-shaped effect was observed for Chl *a,* with high and low concentrations favouring higher diversity.

7. The diversity and species richness of cephalopod communities increased towards the shelf break and upper slope, decreasing afterwards with depth.

8. In contrast to previous studies comparing various data sources, results of this thesis did not support any clear latitudinal or longitudinal gradient in Mediterranean cephalopod diversity.

9. In spite of claims of overfishing and biodiversity loss, Mediterranean cephalopod diversity did not show any significant trend during the last 20 years.

10. Populations of *Octopus vulgaris* and *Illex coindetii* followed a common rising abundance trend in both sub-basins, suggesting that the main drivers of population dynamics act synchronically along the Mediterranean Sea.

11. In the western basin, species are grouped at smaller scale according to spatial differences in environmental variability, whereas in the eastern basin, populations are likely structured at larger spatial scales, as the different eastern sub-areas followed a common abundance trend over the last 20 years.

12. Inter-annual changes of temperature affected *Octopus vulgaris* abundances, while *Illex coindetii* abundances depended on the geographical variations in temperature.

13. High Chl *a* concentration negatively influenced the abundance of *O. vulgaris* and *I. coindetii*, which could be attributed to unsuccessful food competition with fish.

14. Attending to temperature and productivity predictions based on different scenarios established by the Intergovernmental Panel on Climate Change, our results foresee higher impacts on cephalopod community composition in the western than in the eastern basin. Changes in diversity and species abundance will likely differ between different sub-basins.

SECTION II

15. Populations of the cuttlefish *Sepia officinalis* from the Balearic Islands showed a rising abundance trend from 1970 till 2009. During this period, cuttlefish fishing yields were exclusively influenced by local weather conditions and sea surface temperature from a large set of environmental drivers investigated.

16. Population dynamics of cuttlefish from the Balearic Islands are characterised by strong seasonal variations and showed a regime shift during the early 1980s, coinciding with changes in hydrodynamic conditions in the western Mediterranean basin.

17. The application of depletion models to squid and cuttlefish fisheries using data gathered under the European Union Data Collection Framework showed that the current sampling scheme should be redesigned to allow a proper assessment and management of cephalopod stocks in European waters.

18. As cephalopods display important inter-annual fluctuations in life history traits and demographic rates, a weekly or fortnightly biological sampling during the entire population depletion period is required.

19. Even though evidence suggests that Mediterranean cephalopod stocks are not sustainably fished, their monitoring, assessment and management are still missing. However, these measures are of eminent importance in a situation where most cephalopod studies suggest a future rise of cephalopods' ecological importance.

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